Maija E. Marushchak

Carbon Dioxide, Methane and Nitrous Oxide Balance of Subarctic Tundra from Plot to Regional Scales

UNIVERSITY OF
EASTERN FINLAND

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Academic Dissertation
To be presented by permission of the Faculty of Science and Forestry for public examination in the
Auditorium TTA in Tietoteknia Building at the University of Eastern Finland, Kuopio, on 31 January
2014, at 12 o'clock.

Department of Environmental Science

Author´s address: Maija E. Marushchak
                       University of Eastern Finland
                       Department of Environmental Science
                       Bioteknia 2
                       P.O. Box 1627
                       FI-70211 KUOPIO
                       email: maija.marushchak@uef.fi

Supervisors: Professor Pertti J. Martikainen, Ph.D.
                       University of Eastern Finland
                       Department of Environmental Science
                       Bioteknia 2
                       P.O. Box 1627
                       FI-70211 KUOPIO
                       email: pertti.martikainen@uef.fi

                       Christina Biasi, Ph.D.
                       University of Eastern Finland
                       Department of Environmental Science
                       Bioteknia 2
                       P.O. Box 1627
                       FI-70211 KUOPIO
                       email: christina.biasi@uef.fi

Reviewers: Professor Steve Frolking, Ph.D.
                       University of New Hampshire
                       Joint Appointment Department of Earth Sciences
                       Institute for the Study of Earth, Oceans, and Space
                       Durham, New Hampshire, USA
                       email: steve.frolking@unh.edu

                       Nick Ostle, Ph.D.
                       Lancaster Environment Centre
                       Centre for Ecology & Hydrology
                       Lancaster, UK
                       email: no@ceh.ac.uk

Opponent: Professor Torben Christensen, Ph.D.
                       Lund University
                       Department of Physical Geography and Ecosystems Analysis
                       Centre for Studies of Carbon Cycle and Climate Interactions
                       Lund, Sweden
                       email: Torben.Christensen@nateko.lu.se

ABSTRACT:

At present, the northern tundra biome acts as a sink of carbon dioxide (CO_2) and a source of methane (CH_4). In the future, warming and associated permafrost thaw may increase the release of greenhouse gases from tundra soils to the atmosphere, which would be a positive feedback for the climate warming. At the same time, warmer temperatures may lead to increased C sink in the arctic vegetation. Despite the increased attention on tundra gas exchange during the recent years, there are still large uncertainties even concerning the present day greenhouse gas balance.

The aim of this work was to determine the regional CO_2, CH_4 and nitrous oxide (N_2O) balance and total radiative impact of a subarctic tundra landscape on an annual basis. The most of the data was collected at a site located on discontinuous permafrost zone in Northeast European Russia (67°03′N, 62°57′E, 100 m a.s.l.). Fluxes were measured at the plot scale with chamber and gas gradient techniques on all important land cover types and spatially extrapolated over a region of 98.6 km^2 using high-resolution satellite data. The spatially extrapolated plot scale fluxes were verified at landscape scale against eddy covariance measurements of CO_2 and CH_4 before upscaling to the regional level.

On an annual basis the study region acted as a net CO_2 sink of 41 ± 57 g C m^{-2}, a CH_4 source of 5.0 ± 1.3 g C m^{-2} and a N_2O source of 5.8 ± 7.1 mg N m^{-2}. When expressed as CO_2-equivalents over a 100-year time horizon this sums up to a total regional climate forcing of 20 ± 214 g CO_2-eq m^{-2}, meaning a neutral impact on the climate during that year. Leaf area index of vascular plants explained well the large spatial variability observed in the CO_2 fluxes across the landscape, and also correlated positively with CH_4 emissions from tundra wetlands: willow stands and fens. These wetland types were responsible for 99% of the regional CH_4 release. Measurements of N_2O fluxes at the main study site and Finnish palsa mires revealed a previously unknown, strong source of this gas: bare peat surfaces on permafrost peatlands that are created by physical processes related with harsh climate. The other land cover types showed negligible N_2O release, which is in line with previous studies in high-latitude ecosystems. The high emissions from bare peat resulted from a combination of factors favouring both nitrification and denitrification: low C:N ratio of peat, lack of vegetation and intermediate moisture content.

The heterogeneity in gas exchange across subarctic terrain observed in this study stresses the great importance of accurate spatial extrapolation for producing meaningful regional flux estimates. Due to the large variability between the land cover types, the long-term climate change response of GHG balance will be largely determined by changes in the landscape composition. For example, the relative coverage of peat plateaus vs. wet peatlands, determined by permafrost distribution, is important since these peatland types have contrasting fluxes with respect to all the three GHGs.

TIIVISTELMÄ (ABSTRACT IN FINNISH):

Pohjoinen tundra-alue toimii nykyisin hiilidioksidin (CO_2) nieluna ja metaanin (CH_4) lähteenä. Tulevaisuudessa ilmaston lämpenemisen ja ikiroudan sulamisen myötä kasvihuonekaasujen vapautuminen tundran maaperästä voi lisääntyä, millä olisi ilmaston lämpenemistä edelleen kiihdyttävä vaikutus. Toisaalta korkeammat lämpötilat voivat johtaa lisääntyneeseen hiilen sidontaan tundrakasvillisuuteen. Vaikka kiinnostus pohjoisten alueiden kasvihuonekaasuvirtoja kohtaan on lisääntynyt viime vuosina, liittyy tundran tämänhetkiseenkin kasvihuonekaasutaseeseen suuria epävarmuuksia.

Tämän työn tarkoituksena oli määrittää subarktisen tundra-alueen vuotuinen CO_2, CH_4 ja typpioksiduulitase (N_2O) sekä säteilypakote. Suurin osa aineistosta kerättiin epäjatkuvan ikiroudan vyöhykkeellä Luoteis-Venäjällä sijaitsevalla tutkimusalueella (67°03'N, 62°57'E, 100 m mpy). Kaasuvirtoja mitattiin kammio- ja kaasugradienttitekniikoilla kaikista tärkeimmistä maanpeitetyypeistä ja tulokset yleistettiin laajemmalle alueelle korkean resoluution satelliittiaineistoja käyttäen. Kaasuvirtojen spatiaalinen yleistys tarkistettiin ensin vertaamalla sitä maisematasolla kovarianssimenetelmällä mitattuihin CO_2 and CH_4 virtoihin, minkä jälkeen se laajennettiin kattamaan koko 98.6 km²:n tutkimusalue.

Vuositasolla tutkimusalue sitoi hiilidioksidia 41 ± 57 g C m^{-2} ja päästi metaania 5.0 ± 1.3 g C m^{-2} ja typpioksiduulia 5.8 ± 7.1 mg N m^{-2}. Hiilidioksidiekvivalentteina ilmaistuna koko tutkimusalueen kumulatiivinen ilmastopakote 100 vuoden tarkastelujaksolla oli tutkimuksen tekovuotena 20 ± 214 g CO_2-eq m^{-2}, mikä tarkoittaa neutraalia vaikutusta ilmastoon. Putkilokasvien lehtialaindeksi selitti hyvin CO_2-virroissa havaittua suurta alueellista vaihtelua, ja se korreloi positiivisesti myös tundrakosteikkojen CH_4-päästöjen kanssa. Kosteikot – lettosuot ja pajukot – tuottivat 99 % alueellisesta CH_4-päästöstä. Typpioksiduulivuon mittauksissa venäläisellä tutkimusalueella sekä suomalaisilla palsasoilla paljastui aiemmin tuntematon, voimakas N_2O:n lähde: ikiroutasoilla sijaitsevat paljaat turvepinnat, jotka ovat syntyneet ankaraan ilmastoon liittyvien fysikaalisten prosessien tuloksena. Muissa maanpeitetyypeissä ei esiintynyt N_2O-päästöjä, mikä vastaa aiempia tutkimustuloksia tundran N_2O-dynamiikasta. Korkeat N_2O-päästöt paljailta turvepinnoilta ovat seurausta erilaisten sekä nitrifikaatiota että denitrifikaatiota suosivien tekijöiden yhteisvaikutuksesta. Näitä tekijöitä ovat turpeen alhainen C:N-suhde, kasvillisuuden puuttuminen ja riittävä, muttei liian suuri kosteuspitoisuus.

Tässä tutkimuksessa havaitut suuret alueelliset vaihtelut subarktisen tundran kaasuvirroissa korostavat tarkan spatiaalisen yleistyksen tärkeyttä alueellisia kaasutaseita laskettaessa. Koska kasvihuonekaasuvirrat vaihtelevat suuresti maanpeitetyyppien välillä, kaasutaseen vaste ilmastonmuutokseen määräytyy pitkällä tähtäimellä maanpeitetyyppien levinneisyydessä tapahtuvien muutosten perusteella. Esimerkiksi ikiroudassa olevien kuivien soiden ja märkien tundrakosteikkojen suhteellisella levinneisyydellä on suuri merkitys, sillä näillä suotyypeillä on täysin toisistaan poikkeava kasvihuonekaasudynamiikka kaikkien kolmen tässä työssä tutkitun kaasun osalta.

Acknowledgements

LIST OF ABBREVIATIONS

AL	Active layer depth
EC	Eddy covariance
ER	Ecosystem respiration
GHG	Greenhouse gas
GP	Gross photosynthesis
GWP	Global warming potential
LAI	Leaf area index
LCC	Land-cover classification
NEE	Net ecosystem CO_2 exchange
RF	Radiative forcing
WT	Water table depth

LIST OF THE ORIGINAL PUBLICATIONS

This dissertation is based on the following original publications:

Chapter 2.   Maija E Marushchak, Isabell Kiepe, Christina Biasi, Vladimir Elsakov, Thomas Friborg, Torbjörn Johansson, Henrik Søgaard, Tarmo Virtanen, Pertti J Martikainen. 2012. Carbon dioxide balance of subarctic tundra from plot to regional scales. *Biogeosciences* **10**: 437-452, doi: 10.5194/bg-10-437-2013.

Chapter 3.   Thomas Friborg, Maija E Marushchak, Christina Biasi, Daniel Grube Pedersen, Mathias Herbst, Torbjörn Johansson, Isabell Kiepe, Saara E Lind, Pertti J Martikainen, Tarmo Virtanen, Henrik Søgaard. Methane dynamics in warming tundra of Northeast European Russia. Manuscript.

Chapter 4.   Maija E Repo, Sanna Susiluoto, Saara E Lind, Simo Jokinen, Vladimir Elsakov, Christina Biasi, Tarmo Virtanen, Pertti J Martikainen. 2009. Large N_2O emissions from cryoturbated peat soil in tundra. *Nature Geosci* **2**: 189 – 192. doi: 10.1038/NGEO434.

Chapter 5.   Maija E Marushchak, Antti Pitkämäki, Hannu Koponen, Christina Biasi, Matti Seppälä, Pertti J Martikainen. 2011. Hot spots for nitrous oxide emissions found in different types of permafrost peatlands. *Glob Change Biol* **17**: 2601–2614. doi: 10.1111/j.1365-2486.2011.02442.x.

AUTHOR'S CONTRIBUTION

Chapter 2. The author Maija E Marushchak (née Repo) contributed to the design of the study. She carried the main responsibility for data collection and processing related to the plot scale CO_2 fluxes, and for the data integration between the groups. The author wrote the first version of the manuscript together with Isabell Kiepe and Tarmo Virtanen, after which the other co-authors contributed to the writing process.

Chapter 3. The author contributed to the design of the study. She carried the main responsibility for data collection and processing related to the plot scale CH_4 fluxes, and contributed substantially to writing of the manuscript.

Chapter 4. The author designed the study with Pertti Martikainen and was mainly responsible for data collection and processing. She wrote the first version of the manuscript together with Pertti Martikainen and Christina Biasi, after which the other co-authors contributed to the writing process.

Chapter 5. The author contributed to the study design, and was mainly responsible for data collection and processing, and writing of the manuscript.

Contents

1 General introduction

1.1 ARCTIC CARBON AND NITROGEN POOLS

Arctic ecosystems store a huge amount of carbon (C) and nitrogen (N) in their soils. This soil organic matter (SOM) pool has been accumulated in cold and humid conditions that limit decomposition of organic matter. Permafrost regions with soils that remain below 0°C for at least two consecutive years occupy 18.8 million km^2 of the Northern Hemisphere, 35 % of which is located in Eurasia (Tarnocai et al. 2009), particularly in Russia (Anisimov and Reneva 2006). The C pool in these northern permafrost soils is estimated as 1024 Pg (in 0 to 3 m), which is about 40 % of the global soil C pool (Tarnocai et al. 2009) and more than the C pool in the atmosphere. The available estimate of the tundra N pool by Post et al. (1985), 3.7 Pg, is limited to the upper 1 m and is likely an underestimate. Using the C pool estimate by Tarnocai et al. (2009) and C:N ratio of 20-40 of soil, the size of tundra soil N pool would be 26-51 Pg. As much as 90 % of the high-latitude C pool (Tarnocai et al. 2009) and, similarly, a large part of soil N, is currently in permanently frozen soil layers. These permafrost C and N pools are largely protected from soil microbial activities, but there is a considerable concern that they will become accessible for microbial processes if the soil will thaw.

About 19% of the Northern permafrost areas is covered by peatlands. Peatland ecosystems often have the highest C content per unit area among different land forms in the mosaique-like permafrost terrain (up to 150-195 kg C m^{-2} in 0-3 m; Tarnocai et al. 2009, Hugelius et al. 2011). Particularly high C stocks in the Subarctic can be found in peat plateaus, large flat-topped expanses of permafrost peatlands heaved up by frost (French, 2007). A major part of these peat deposits has been accumulated during warmer climatic conditions in the early and mid Holocene before cooling and onset of permafrost slowed down the rate of peat accumulation (Oksanen et al. 2001, Sannel and Kuhry 2009). On upland tundra underlain by mineral soils the C content is usually lower than in tundra peatlands, but very high C stocks have been found in soils affected by cryoturbation (up to 160 kg C m^{-2} in 0-3 m; Bockheim 2007, Tarnocai et al. 2009). Cryoturbation means soil movement and mixing due to frost action (French, 2007). This process buries fresh organic matter to deeper soil layers, where decomposition is limited by low temperatures and lack of oxygen. As a result, cryoturbation usually enhances soil C storage in upland soils (Bockheim 2007, Kaiser et al. 2007).

Plant biomass typically represents only a small part of total C and N pool in high-latitude ecosystems (Bazilevich, 1993, Hugelius et al. 2011). The main factors limiting plant growth in tundra are low temperatures during the growth period, high abundance of wet soils and long snow cover, and resulting low nutrient availability due to slow turn-over of organic matter (Shaver and Chapin 1995, Shaver et al. 2001). The nutrient limitation of tundra ecosystems has been

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demonstrated by stimulation of plant growth by N and P additions (Jonasson et al. 1999, Johnson et al. 2000, Arens et al. 2008).

1.2 CLIMATE CHANGE IN THE ARCTIC

Many changes are anticipated in the arctic environment with climate change, one very relevant being the threat to the large C and N pools in northern permafrost soils. Enhanced release of C and N from high-latitude ecosystems to the atmosphere could lead to a positive feedback loop further accelerating climate change. Global climate models predict for arctic areas stronger warming than for the globe on average and increased precipitation (Kattsov et al., 2005). By 2100, the annual mean temperatures are predicted to increase by 5-7°C and the precipitation by 5-35 %, the largest changes taking place during autumn and winter. Indications of warming have already been observed: The period 2005-2010 was warmer in the Arctic than any five-year period since the surface air temperature measurements began in the late 19th century (AMAP, 2011). Further, reduced snow cover, higher permafrost temperatures and deeper active layers have been observed across the pan-arctic region during the past decades (AMAP, 2011). These changes are affecting the functioning and composition of high-latitude ecosystems in a very complex way, not yet sufficiently understood.

1.3 GREENHOUSE GAS EXCHANGE IN HIGH-LATITUDE ECOSYSTEMS

From the three most important long-lived GHGs, carbon dioxide (CO_2) is the one that has been most broadly studied is tundra ecosystems. This can be justified, since CO_2 is causing the largest radiative forcing (RF) of the three gases, thus being the strongest contributor to global warming (63% of the RF caused by long-lived GHGs; IPCC, 2007). Due to the much lower atmospheric concentrations, the RF of methane (CH_4) and nitrous oxide (N_2O) is lower than that of CO_2 (18 and 6 % of the RF caused by long-lived GHGs, respectively; IPCC, 2007), although they are stronger GHGs per mass unit. According to the global warming potential (GWP) approach (IPCC, 1990), a unit mass pulse emission of CH_4 causes 25 higher climate forcing than that of CO_2 in 100years time, the same coefficient for N_2O being 298 (IPCC, 2007). The GWP is dependent on the reference period due to different atmospheric life-times of the GHGs. Due to the shorter lifetime of CH_4 (12 years), its relative importance compared to N_2O (lifetime 114 years) and CO_2 is larger at a shorter time horizon.

The gross fluxes of CO_2 in tundra can be orders of magnitude higher on a mass basis than those of CH_4 and N_2O (Heikkinen et al. 2004, Brummell et al. 2012). However, the net flux of CO_2 can be close to zero and then the uptake or release of the two other gases becomes important for the total climate forcing. Flux assessments including all three gases have been published from many ecosystem types, e.g., agricultural lands (Soussana et al. 2007), tropical and temperate forests (Butterbach-Bahl et al. 2004, Luo et al. 2012), pristine and managed boreal peatlands

(reviewed by Maljanen et al. 2010), savanna (Hao et al. 1988) and Antarctic soils (Gregorich et al. 2006), but comprehensive reports on full GHG balance of northern tundra have been lacking so far.

1.3.1 Carbon dioxide and methane fluxes in terrestrial ecosystems

There is a high variability in C fluxes of high-latitude ecosystems both in time and space, but according to a recent meta-analysis the arctic tundra as a whole acts as a net C sink (110 Tg C yr^{-1}; McGuire et al. 2012). Carbon dioxide is the main component of the atmospheric C exchange of tundra (e.g., Fan et al. 1992, Heikkinen et al. 2004, Corradi et al. 2005). Tundra wetlands often are strong CO_2 sinks (e.g., Heikkinen et al. 2002, 2004), while the CO_2 balance of upland tundra with mineral soil is typically closer to zero, and can switch between a C sink and source from year to year (Heikkinen et al. 2004, Lund et al. 2010).

The net response of tundra CO_2 balance to the climate change is still highly uncertain despite the increasing scientific interest the topic has received during the last decades (McGuire et al. 2009). The possible change in the balance results from the sum of the changes in the two opposite gross fluxes: gross photosynthesis (GP) and ecosystem respiration (ER). Many studies suggests that higher temperatures and associated permafrost thaw will enhance decomposition of SOM, increasing losses of old soil C as CO_2 to the atmosphere (e.g., Dorrepaal et al. 2009, Schuur et al. 2009, Vogel et al. 2009, Natali et al. 2011). However, the increased respiration can be partly or fully compensated by the concurrent increase in CO_2 uptake by plants (Vogel et al. 2009, Qian et al. 2010, Natali et al. 2011, Trucco et al. 2012). So called arctic greening, caused by expansion and better growth of deciduous shrubs, has been observed during the last decades (Sturm et al. 2001, Forbes et al. 2010). Besides the direct positive effect of warmer temperature, growth of fast-growing plant species is stimulated by better nutrient availability related to faster mobilization of nutrients from soil organic matter (Chapin et al. 1995).

The results from multiannual studies from arctic and subarctic ecosystems are partly contradictory to each other with respect to environmental controls of the ecosystem CO_2 sink. Earlier snow-melt and longer growing season led to higher seasonal net uptake of CO_2 in a subarctic fen in Northern Finland (Aurela et al. 2004), but not in a graminoid tundra in Northeastern Siberia (Parmentier et al. 2011). In the later study, warm temperatures during growing season promoted GP but also ER, so that the net effect on ecosystem CO_2 sink was insignificant. In a high-arctic heath in Greenland warmer temperatures initially increased ecosystem C sink but only up to a certain limit, above which ER kept increasing while GP leveled off (Groendahl et al. 2007, Lund et al. 2012). These results show that, similarly to the present C balance of tundra, also its response to climate warming varies a lot between various tundra types, and it is important to account for the whole range of this variability when planning studies on tundra C balance.

Although CH_4 comprises a smaller part of the gross C fluxes in the Arctic and many abundant tundra surfaces have negligible CH_4 fluxes, the tundra biome is a globally important source of CH_4 due to high emissions from tundra wetlands (19 Tg C yr^{-1}; McGuire et al. 2012). Methane is produced in water-saturated layers of wetlands by obligately anaerobic methanogenic archaea (Whalen 2005). Depending

on the position of ground water table and the depth of the aerobic soil layer, up to 90% of the produced CH_4 can be oxidized to CO_2 by methanotrophic bacteria before entering the atmosphere (Oremland and Culbertson 1992). Permafrost distribution largely determines the CO_2 and CH_4 fluxes from subarctic peatlands. On frozen palsa and peat plateau surfaces aerobic conditions and ombrotrophy cause low emissions of CH_4 and small net flux of CO_2, while unfrozen fens with high-water tables show high CH_4 efflux and CO_2 uptake (Nykänen et al. 2003, Heikkinen et al. 2004). Thus, permafrost thaw resulting in increased coverage of wet peatland surface has strong consequences on regional C exchange (Johansson et al. 2006). Small uptake of CH_4 has been observed in tundra and forest tundra soils (Christensen et al. 1997, Sjögersten and Wookey 2002, Flessa et al. 2008).

1.3.2 Carbon dioxide and methane fluxes from lakes and ponds

Arctic lakes and ponds usually show release of CO_2 and CH_4 to the atmosphere (Kling et al. 1991, Kling et al. 1992, Bastviken et al. 2011), fuelled by C input from surrounding terrestrial ecosystems by leaching and erosion. So-called thermokarst lakes, formed by degradation of permafrost, are known as hot spots of arctic CH_4 emissions (Walter et al. 2006, Blodau et al. 2008, Desyatkin et al. 2009, van Huissteden et al. 2011). The high CH_4 emissions from thermokarst lakes can be explained by the quality of C substrates: C released from permafrost C pool at thawing can be fairly undecomposed and, therefore, labile (Zimov et al. 1997, Walter et al. 2006). Trace gas emissions from lakes can take place by diffusion or ebullition that means abrupt gas release from the sediment as bubbles. While ebullition is only a minor pathway of CO_2 emissions from water-bodies, it is highly important for CH_4, comprising up to 95% of the total CH_4 flux from thermokarst lakes (Walter et al. 2006). Some of the reported lake CH_4 emissions without the ebullitive CH_4 flux component (Kling et al. 1992, Heikkinen et al. 2004) are likely underestimates.

As lakes and ponds represent sources of terrestrially fixed C to the atmosphere in high-latitude landscapes that generally act as C sinks (Bastviken et al. 2011), changes in their abundance are relevant for the regional C balance. Remote sensing studies from different parts of the Arctic tell different stories on the thermokarst lake dynamics during the second half of the 20th century. While increase in the lake area has been observed in some permafrost regions (Riordan et al. 2006), the number and area of water bodies has decreased in others due to improved drainage as a result of permafrost thaw (Smith et al. 2005, Jones et al. 2011). The formation of thaw lakes and ponds is not always indicative for unidirectional changes in the permafrost coverage. As a part of the normal thermokarst dynamics the development of thermokarst lakes and ponds is often followed by re-growth and permafrost aggradation, making the increase in CH_4 (and CO_2) release only temporary (van Huissteden et al. 2011).

1.3.3 Nitrous oxide fluxes

The few studies published on N_2O exchange in permafrost soils usually report small or negligible emissions (Christensen et al. 1999, Ludwig et al. 2006, Rodionow et al. 2006, Ma et al. 2007, Takakai et al. 2008, Siciliano et al. 2009). Recently, N_2O uptake

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has been reported in polar desert soils with relatively low soil moisture (Stewart et al. 2012). Aerobic nitrification (oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-)) and anaerobic denitrification (reduction of NO_3^- and NO_2^- to nitric oxide (NO), N_2O and dinitrogen (N_2) gas) are the two main processes responsible from N_2O production in soils (Richardson et al. 2009). The key reason for the low N_2O emissions from pristine arctic ecosystems in general is shortage of mineral N for microbial processes due to the slow mineralization of organic matter in cold climates (Nadelhoffer et al. 1991) and low N deposition (Dentener, 2006). However, studies on N_2O exchange have been mostly carried out on upland tundra with mineral soil, while tundra peatlands have been ignored. Boreal peatlands often show N_2O uptake in pristine stage, but large emissions are induced by draining them for economic use (Martikainen et al. 1993, Regina et al. 1996, Maljanen et al. 2010). Lowering of the water level enhances mineralization of organic N from peat that previously has been preserved in anaerobic conditions. As a result, availability of mineral N for soil microbial activity, including N_2O production, increases. On this background, permafrost peatlands with their large organic N reservoirs and oxic conditions in the upper peat profile due to uplifting by permafrost appear as potential sources of N_2O. Moreover, peat plateaus have patterned ground features completely lacking vegetation (see Section 1.6), where soil microbes do not have to compete for inorganic N with plants. In this work, N_2O fluxes were investigated from all main land cover types of a subarctic landscape, but a special focus was on peat plateau environment due to the facts discussed above.

1.4 METHODS USED TO MEASURE TRACE GAS EXCHANGE IN TUNDRA

Previous studies show that GHG fluxes in tundra exhibit high seasonal (e.g., Laurila et al. 2001, Wagner et al. 2003), interannual (e.g., Rennermalm et al. 2005, Humphreys and Lafleur 2011) and spatial (e.g., Heikkinen et al. 2004) variability. The measuring techniques used in flux studies in tundra should account for this variability in a satisfactory way. At the same time, researchers face logistical difficulties when working in remote arctic areas, and are often forced to make compromises with respect to selection of the measuring techniques and duration and timing of the field campaigns. Due to the limitations related to power supply, accessibility and harsh conditions during the winter season, most of the published GHG flux studies from arctic and subarctic ecosystems are limited to the summer growing season (McGuire et al. 2012), but the number of reports with year-round flux measurements is increasing (e.g., Aurela et al. 2004, Vogel et al. 2009, Jackowicz-Korczynski et al. 2010).

The most widely used techniques for measuring trace gas exchange in tundra are the micrometeorological eddy covariance (EC) method (e.g., **CO_2:** Moncrieff et al. 1997, Nordstroem et al. 2001, Corradi et al. 2005, Lafleur and Humphreys 2008, Lund et al. 2012; **CH_4:** Sachs et al. 2008, Wille et al. 2008; **CO_2 & CH_4:** Fan et al. 1992) and manual or automatic flux chambers (e.g., **CO_2:** Shaver et al. 1998, Shaver et al. 2007; **CH_4:** Reeburgh et al. 1998, Sachs et al. 2010; **CH_4 & CO_2:** Christensen et al. 2000, Heikkinen et al. 2002, 2004; **N_2O:** Ma et al. 2007, Siciliano et al. 2009). Studies

where eddy covariance and chambers have been used in parallel are far more rare (Soegaard et al. 2000, Zamolodchikov et al. 2003, Fox et al. 2008, Sachs et al. 2010).

In this work, a combination of manual chambers operated by University of Eastern Finland (CO_2, CH_4 and N_2O; Chapters 2, 3, 4 and 5) and eddy covariance operated by University of Copenhagen (CO_2, CH_4; Chapters 2 and 3) was used. Table 1 summarizes the strengths and weaknesses of the two flux measuring techniques. With integrative micrometeorological EC technique it is possible to obtain continuous, integrative flux over a source area of 0.1-1 km² and catch the short-term variations in gas exchange, but extrapolation of EC data over larger regions is dependent on representative site selection that is not always feasible (Kim et al. 2006).

Table 1 *Comparison of the two measuring techniques used to measure GHG fluxes in terrestrial ecosystem in this study.*

Measuring technique	
Eddy covariance	+ good temporal resolution
	+ better areal coverage than that of chamber technique
	+ minimal disturbance of the ecosystem studied
	- limited information on spatial variability in the fluxes
	- limitations in operating conditions
	- difficulties to extrapolate the fluxes to a larger area
	- high cost
Manual chamber technique	+ good spatial resolution
	+ inexpensive, independent of mains power
	+ possibility to relate fluxes to the environmental conditions at microsite level
	+ allows extrapolation of the fluxes to larger areas
	- high demand for manpower
	- low temporal resolution
	- low areal coverage if spatial extrapolation is not done
	- disturbance caused to the studied system

On the other hand, chamber measurements give information on spatial variability in fluxes of different functional ecosystem types and their dependence on local environmental conditions. This kind of data are particularly useful when the aim is to upscale the flux data to regional estimates in highly fragmented environments like tundra (Heikkinen et al. 2004, Flessa et al. 2008, Fox et al. 2008). Automated chambers represent an intermediate variant between the EC and manual chamber techniques with respect to temporal and spatial resolution and cost. The decision between manual and automated chambers was made in favor of the manual ones based on independence of mains power, lower cost and possibility to include a large number of microsites (10) in order to cover all the dominant land cover types in the studied landscape.

During the snow cover fluxes were determined using the snow gradient technique, where flux is calculated from the concentration gradient between the snow-pack and the atmosphere using gas-specific diffusion coefficients

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(Sommerfeld et al. 1993; Chapters 2, 3, 4 and 5). Maljanen et al. (2003) showed on boreal organic soils that this measuring technique and chamber method give rather similar flux rates. The winter measurements were few in number but caught different periods of winter season: autumn freezing in October, mid-winter in January and March and spring thaw in May-June.

In addition to the terrestrial ecosystems, gas exchange was measured from thermokarst lakes (Chapters 2 and 3). The different emission pathways, diffusion and ebullition, were accounted for by using a combination of two measuring techniques. Diffusive emissions were determined with a thin boundary layer (TBL) method, where flux is calculated from gas concentration in the surface water and local wind speed (Liss and Slater 1974). Permanently installed submerged gas collectors, similar to those used by Huttunen et al. (2001), were used for measuring the ebullitive flux. The combination of these two methods was proved suitable for measuring CO_2 and CH_4 dynamics in small peatland lakes in Western Siberia (Repo et al. 2007).

1.5 AREAL INTEGRATION OF GREENHOUSE GAS FLUXES

For correct estimation of regional GHG balances it is as important to extrapolate the collected data correctly as it is to perform accurate measurements. This requires representative selection of study sites, but also information on the spatial extent of various land cover types. The term land cover type is used in this work to refer to an ensemble of vegetation and underlying soil.

For a heterogeneous environment like tundra correct spatial upscaling of the fluxes is a demanding task. In earlier studies, regional flux estimates of tundra have been based on i) modeling approaches using remote sensed or measured explanatory variables (e.g., normalized difference vegetation index (NDVI), soil moisture, temperature, thaw depth) and measured flux data (Oechel et al. 2000, Stoy et al. 2009, Lee et al. 2012) or ii) land cover classification and weighing the fluxes of different landscape units by their coverage (Heikkinen et al. 2004, Flessa et al. 2008, Fox et al. 2008, Sachs et al. 2010). The spatial data for previous upscaling exercises have been obtained from either Landsat satellite images (resolution 30 m, scene size ~30 000 km²; Soegaard et al. 2000, Heikkinen et al. 2004), QuickBird satellite images (resolution 0.6-2.4 m, scene size 100 km²; Flessa et al. 2008), aerial photography (resolution 0.5 m; Sachs et al. 2010) or ground observations in a regular grid (resolution 5 m; Fox et al. 2008, Lee et al. 2011). In practice, there is often a trade-off between the areal extent and the spatial resolution. Landsat images are suitable for broad vegetation mapping, but they are not detailed enough to detect the small scale variability typical for tundra (Laidler and Treitz 2003). The high-resolution QuickBird satellite images used in this study provide a rather optimal combination of a scene size of a regional scale and a resolution high enough to realistically represent the tundra landscape.

While the above-mentioned extrapolation studies have operated in two scales (plot-to-landscape or plot-to-regional), the nested study design of the present work included three scales: flux measurements in two sequential scales and extrapolation

to the regional scale using high-resolution QuickBird satellite data. The landscape level was used as an intermediate step that allowed verification of the plot scale CO_2 and CH_4 fluxes obtained by chamber and gas gradient techniques against EC fluxes for before extrapolating them to the regional level (Chapters 2 and 3).

1.6 STUDY SITES

The most of the data for this thesis were collected at a southern tundra site located near the settlement of Seida in the Komi Republic, Northeast European Russia (67°03′N, 62°57′E, 100 m a.s.l.; Fig. 1). The Seida site was selected as one of the two intensive flux sites of a EU-funded research project that aimed at quantifying the C budget in Northern Russia in past, present and future (CARBO-North; see http://www.carbonorth.net/). The mean annual air temperature in the study region is –5.6 °C and the mean annual precipitation is 501 mm (long-term averages for 1977-2006, data from Vorkuta station (67°48′N, 64°01′E, 172 m a.s.l.); Komi Republican Center for Hydrometeorological and Environmental Monitoring). The study site is located close to the northern tree line, and has isolated forest patches with spruce and fell birch as dominant tree species. It is underlain by discontinuous permafrost (permafrost coverage of 50-90%). The location on the southern edge of the permafrost zone and proximity to the forest border make this site interesting from the climate change point of view: Rapid changes can be expected with respect to vegetation cover and permafrost distribution. The region is already experiencing permafrost warming and thaw, as reported by Oberman (2008).

Figure 1 *Location of study sites: The main study site Seida in Komi Republic, Russia (67º03′N, 62º57′E) and palsa mires Luovdijeäggi (69º35′N, 26º11′E), Tsulloveijeäggi (69º35′N, 26º12′E) and Vaisjeäggi (69º49′N, 27º10′E) in Utsjoki, Finnish Lapland. The dashed line indicates the Arctic Circle.*
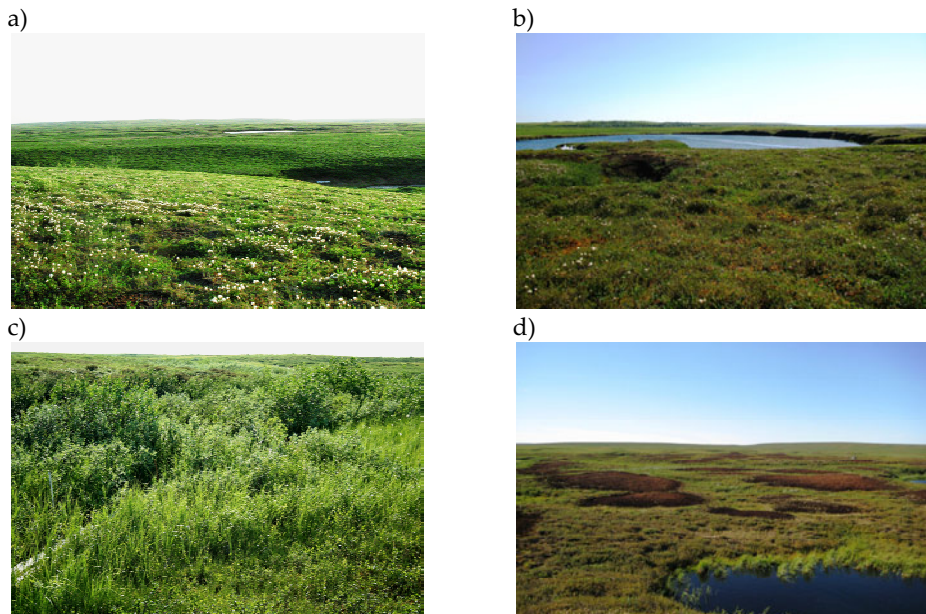
Figure 2 *The dominant land cover types in the main study region. a) Upland tundra heath; b) Tundra bog vegetation on peat plateau and a thermokarst lake; c) Willow stand and mesotrophic fen; d) Bare peat surface on peat plateaus. Photographs by Pyotr Ievlev (a, b), Simo Jokinen (c) and Maija Marushchak (d).*

A distinctive characteristic of the study site are peat plateaus, massive permafrost peatlands with up to several meters thick frozen peat deposits (Fig. 2b). They have by far the largest belowground C stocks per unit area in the whole landscape. According to a soil C inventory done at the Seida site, the below ground C stock for the upper 3 m in peat plateaus is 150.8 g C m^{-2}, while the mean for the whole study site is 40.5 g C m^{-2} (Hugelius et al. 2011). In the peat plateaus the peatland surface is heaved up by frost and, as a result, the peat layer above the permafrost table is mostly well drained and overlain by ombrotrophic bog vegetation. The depth of the seasonal thaw, or active layer depth, is shallow in the peat plateaus due to low thermal conductivity of unfrozen, dry peat. Compared to another type of permafrost peatlands, palsa mires existing in milder climate in the sporadic permafrost zone, peat plateaus have more frozen surfaces relative to unfrozen ones (see Chapter 5).

Peat plateaus contain unvegetated peat surfaces, so called peat circles (Fig. 2d). Peat circles are round patches of bare peat partly covered by a thin moss layer but without any vascular plants. The irregular and bumpy peat surface and high ice content during the winter suggest that these surfaces are affected by cryoturbation, soil mixing by frost action (Bockheim and Tarnocai 1998). Wind abrasion of the surface peat leads to formation of bare peat surfaces on palsa mires, and it might be also the initial factor behind the peat circle formation on peat plateaus. Small and

shallow thermokarst lakes, initialized by local thawing of permafrost, are also mostly located within the peat plateau.

Peat plateaus and thermokarst lakes are surrounded by narrow stripes of unfrozen waterlogged fens that act as water conduits in the terrain (Fig. 2c). Fens are typically mesotrophic and have a floating *Sphagnum* mat. Willow stands growing on the low lying parts of the landscape are also typical for the region. They have the highest C stocks in above ground plant biomass of all land cover types except for the small forest stands (Hugelius et al. 2011). Most of the landscape in the region is hilly upland with tundra heath vegetation and thin organic layer underlain by mineral soil (Fig. 2a). These areas have shrub tundra vegetation dominated by *Betula nana, Salix* sp., dwarf shrub, mosses and lichens.

The CO_2 and CH_4 dynamics have been studied earlier with the manual technique in the same region, around 40 km north from the Seida site by Heikkinen et al. (2002, 2004). In addition, Zamolodchikov et al. (2000) measured summer time CO_2 dynamics of different tundra plant communities with manual chambers at two sites located further north from Seida. Nevertheless, Northeast European Russian tundra is underrepresented concerning GHG flux studies and it is lacking a permanent research facility that would provide long term data on trace gas flux dynamics.

Figure 3 *Bare palsa surfaces on Luovdijeäggi palsa mire in Northern Finland. Photograph by Maija Marushchak.*

In addition to the Seida site, N_2O fluxes were measured from three palsa mires, Luovdijeäggi (69º35′N, 26º11′E, 370 m a.s.l.), Tsulloveijeäggi (69º35′N, 26º12′E, 365 m a.s.l.) and Vaisjeäggi (69º49′N, 27º10′E, 295 m a.s.l.), located in the sporadic permafrost zone in Utsjoki, Northern Finland (Fig. 1). This region has a milder climate than the Seida site, with a mean annual air temperature of –1.7 °C and mean annual precipitation of 414 mm (long-term averages for 1962-2006, data from Utsjoki-Kevo station (69°45′N, 27°00′E, 107 m a.s.l.); Finnish Meteorological Institute). Typical palsas on the studied mires are 1 to 3 m high with a diameter of

20 to 50 m (Fig. 3). Vegetation on palsas is small-statured and consists of dwarf shrubs, especially *Empetrum hermaphroditum*, herbs (e.g., *Rubus chamaemorus*), mosses (*Dicranum* spp., *Pleuzerium* spp.) and lichens. A large part of the palsa surface is unvegetated due to wind abrasion that has removed up to several tens of centimetres of peat (Seppälä 2003). Frost boils, small patches of bare soil formed by cryoturbation frequently occur on mineral soils around the palsa mires.

1.7 AIMS OF THE STUDY

The aim of this thesis was to determine the regional GHG balance of a heterogeneous southern tundra landscape. For the first time, N_2O was included in such a regional flux assessment in tundra in addition to CO_2 and CH_4. The specific goals of the study were:

- To understand the spatial variability in the fluxes of CO_2, CH_4 and N_2O, and the factors behind this variability by plot scale measurements based on chamber and gas gradient techniques.
- To verify the accuracy of upscaling of the plot scale fluxes in the landscape scale against integrative eddy covariance measurements.
- To estimate the regional GHG balances by integrating the plot scale fluxes over the study region using high resolution satellite data.
- To assess the relative importance of CO_2, CH_4 and N_2O to the total climate forcing of different land cover types and of the subarctic tundra region, with implications for climate change.

2 Carbon dioxide balance of subarctic tundra from plot to regional scales

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3 Methane dynamics in warming tundra of Northeast European Russia

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4 Large N₂O emissions from cryoturbated peat soil in tundra

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5   Hot spots for nitrous oxide emissions found in different types of permafrost peatlands

6 Regional greenhouse gas balance and net radiative impact of subarctic tundra

6.1 INTRODUCTION

Subarctic tundra is a mosaic of various land cover types - ensembles of vegetation and underlying soil - that alternate within distances from tens to hundreds of meters. This is a result of variation in topography, hydrology and permafrost distribution, factors that are interrelated in complex ways. Different land cover types show strong differences concerning fluxes of the three important green house gases (GHGs), CO_2, CH_4 and N_2O (Chapters 2, 3, 4 and 5). While there are numerous studies on the full atmospheric C balance ($CO_2 + CH_4$) of tundra landscape (e.g., Heikkinen et al. 2002, 2004, Wille et al. 2008, Bäckstrand et al. 2010), there are, to our knowledge, no studies that have included also N_2O in the total GHG balance estimated over an extended period. This can be explained by the assumption that N_2O fluxes are unimportant in pristine high-latitude ecosystems, a concept questioned by recent results showing that some subarctic and arctic soils have potential for high N_2O emissions (Chapters 4 and 5 of this thesis; Elberling et al. 2010). Also N_2O sink capacity has been observed lately in high Arctic soils (Stewart et al. 2012). Furthermore, while many of the earlier studies on tundra greenhouse gas balance have been focused only on certain (dominant) land cover types, in this study the GHG fluxes were determined from all important elements of a heterogeneous subarctic tundra landscape ranging from terrestrial to aquatic, mineral to peat soils, water-logged to dry and from complete lack of vegetation to dense cover of tall shrubs.

This chapter brings together the results of different sub-studies on CO_2, CH_4 and N_2O (Chapters 2 to 5) in order to achieve the ultimate goal of this thesis: estimating the total annual GHG balance and the net radiative impact of the study region of 98.6 km² located in Northeast European Russia in the discontinuous permafrost zone. In order to compare the importance of different GHGs and land cover types, the emissions of different gases were converted to CO_2 equivalents using the GWP approach (IPCC, 1990; Chapter 1.3).

6.2 METHODS

The flux data used to calculate the total regional CO_2 and CH_4 balances are reported in Chapters 2 and 3, respectively. These chapters describe in detail the methods used: chambers and snow gradient methods for terrestrial ecosystems and thin

boundary layer method and bubble gas collectors for lakes. For the regional N_2O flux estimate, the more extensive data set reported in Chapter 5 was used instead of the one snow-free period data reported in Chapter 4. As for CO_2 and CH_4, the growing season N_2O flux is from 2008 (16 June to 2 September; 79 days) and the annual estimate is reported for the period from 6 October 2007 to 5 October 2008. The numbers are somewhat deviating from those reported in Chapter 5, where the growing season flux is the average from 2007 and 2008, and annual flux is the sum of this mean growing season flux and the cold season flux 2007-2008.

A common procedure was needed for extrapolating the plot scale fluxes of different gases to the regional scale. In Chapter 2 the regional CO_2 balance was estimated by two independent upscaling methods: i) by weighing the unit-area fluxes of different land cover types with their percent coverage according to a land cover classification (the LCC approach) and ii) by using the linear dependence between LAI and CO_2 fluxes, observed in the plot scale, and the mean growing season leaf area index (LAI) for the study region obtained by remote sensing (LAI map approach). These two approaches gave rather similar results (see Chapter 2). For calculation of the regional net radiative balance only the results of the LCC approach are used, since it was the method used for upscaling the CH_4 fluxes and directly applicable also for extrapolating N_2O fluxes. When the high N_2O emissions from peat circles were scaled up in Chapter 4, the small N_2O fluxes per unit area from all the other surfaces were set to zero. Here, the actual measured N_2O flux values were used for each land cover type.

The uncertainties for regional estimates were calculated as described in Section 2.7: the standard deviations (SDs) of hourly/daily microsite fluxes were weighed with corresponding area contributions and these area-weighed SDs were summed up over time. Finally, CH_4 and N_2O fluxes were transformed into CO_2-equivalents with the GWP approach (IPCC, 2007) to allow calculation of net radiative balance including all three gases. This approach takes into the account the radiative forcing per mass unit and life-time of different gases. From the three time horizons commonly used in GWP assessments - 20, 100 and 500 years - the intermediate reference period of 100 years was selected here. A shorter time interval would have overemphasized the meaning of CH_4, while a very long time horizon would have been irrelevant considering the time scale of the anticipated climate changes in the subarctic. Thus, the coefficients used to convert mass emissions of CH_4 and N_2O to CO_2 equivalents were 25 and 298, respectively (IPCC, 2007).

6.3 THE REGIONAL CLIMATE FORCING AND THE IMPORTANCE OF DIFFERENT GREEN HOUSE GASES

The regional balance estimates and climate forcing of different GHGs as CO_2 equivalents are summarized in Table 1. On an annual basis the study area acted as a small (and insignificant) sink of CO_2 of -41 ± 57 g C m^{-2} and a small source of CH_4 (5.0 ± 1.3 g C m^{-2}) and N_2O (5.8 ± 7.1 mg N m^{-2}). The annual C balance ($CO_2 + CH_4$) was -36 ± 54 g C m^{-2}. When considering all the three gases the total climate forcing of the study region in the study year was close to zero (20 ± 214 g CO_2-eq m^{-2} yr^{-1}; Table

1), meaning that the effect of the region on the climate was almost neutral. Considering the high interannual variability in the subarctic and arctic GHG fluxes in other studies (e.g., Rennermalm et al. 2005, Humphreys and Lafleur 2011), it is likely that the study region switches between a net sink and source of GHGs from year to year. However, during the growing season from mid June to early September the region was a net sink of GHGs with significantly negative radiative impact of -226 ± 131 g CO_2-eq m^{-2}. Although the measurements carried out during the cold season did not show very high emission peaks, a phenomenon often observed in northern soils (e.g., CO_2: Bubier et al. 2002; CH_4: Mastepanov et al. 2008; N_2O: Maljanen et al. 2009), the large difference between growing season and annual GHG balance indicates high importance of winter. All three GHGs showed emissions during the winter, and when accumulating over the long winter time even small daily fluxes become important (see also Aurela et al. 2002).

Methane has a rather minor role in the total C balance of the studied subarctic landscape: 4% of the net C sink as CO_2 was lost as CH_4-C during the growing season and the annual CH_4-C loss was 12% of the net CO_2-C sink. However, when calculated as CO_2-equivalents the CH_4 emissions reduced the growing season GHG sink by 34%, and overruled the CO_2 sink on an annual basis. The important role of CH_4 for the total radiative impact of northern peatlands is well-known from previous studies (e.g., Friborg et al. 2003, Frolking et al. 2006, Johansson et al. 2006). The results here stress that even if over 80% of the terrain has negligible CH_4 fluxes, CH_4 can still have a great importance for regional climate forcing. The regional N_2O emission was very low, and its importance for the regional radiative impact was marginal.

Table 1 *Regional greenhouse gas (GHG) balance of the study region of 98.6 km². The total GHG balance as CO_2-equivalents, i.e., the net radiative impact was calculated using the GWP approach with a 100-year time horizon (coefficients for CH_4 = 25 and N_2O = 298). Negative values indicate GHG a sink/cooling effect; positive values indicate a GHG source/warming effect.*

	Growing season balance			Annual balance		
	16 June to 2 Sept 2008			6 Oct 2007 to 5 Oct 2008		
CO_2						
g C m^{-2}	-94	±	37	-41	±	57
g CO_2 m^{-2}	-344	±	136	-150	±	208
CH_4						
g C m^{-2}	3.5	±	0.8	5.0	±	1.3
g CO_2-eq m^{-2}	118	±	26	168	±	45
N_2O						
mg N m^{-2}	1.4	±	3.1	5.8	±	7.1
g CO_2-eq m^{-2}	0.6	±	1.4	2.7	±	3.3
TOTAL C BALANCE (CO_2 +CH_4)						
g C m^{-2}	-91	±	34	-36	±	54
TOTAL GHG BALANCE (CO_2 + CH_4 + N_2O)						
g CO_2-eq m^{-2}	-226	±	131	20	±	214
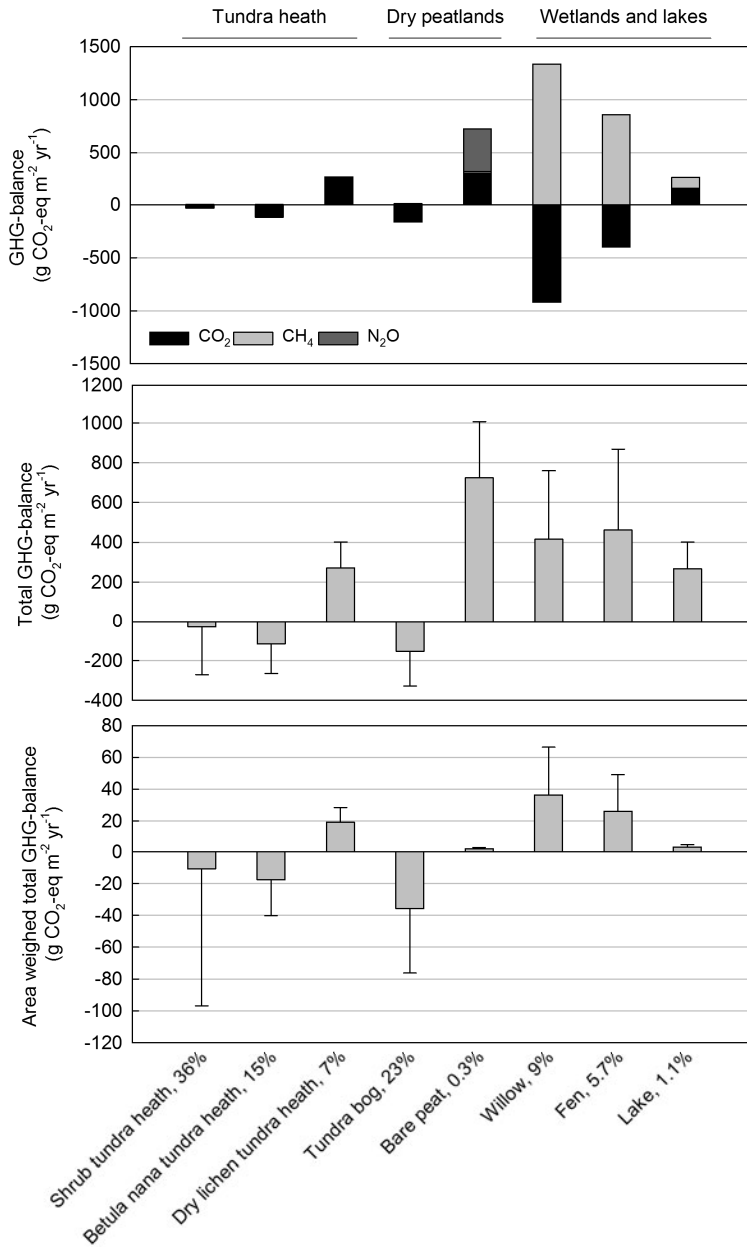
Figure 1 *Radiative impact of different land cover types as CO_2-equivalents over a 100-year time horizon (n = 3- 6). Top: Fluxes of CO_2, CH_4 and N_2O; middle: Total GHG balance including the three GHGs, bottom: GHG balance weighed by area coverage of each land cover type (%), indicated on the x-axis. This representation illustrates the relative importance of different land cover types for regional flux. Negative flux values indicate a GHG sink/cooling effect; positive values indicate a GHG source/warming effect.*

6.4 CLIMATE FORCING OF DIFFERENT LAND COVER TYPES AND THEIR IMPORTANCE FOR THE REGIONAL BALANCE

From the eight land cover types studied only shrub tundra heath, *Betula nana* tundra heath and tundra bog were (insignificant) GHG sinks as CO_2-equivalents on an annual basis (Fig. 1). They were characterized by small net CO_2 uptake rates and very low fluxes of CH_4 and N_2O. However, these three land cover types have high area coverage in the studied terrain, so they were important for the regional climate forcing (Fig. 1). The other five land cover types had a net warming impact on climate, also the wetlands that showed strong C sink but had large CH_4 emissions. The willow stands, covering 8% of the study region, were important to the regional C balance and CH_4 emission due to their high C gas fluxes on a unit area basis (Chapters 2 and 3).

The two extreme land cover types concerning the total climate forcing caused by GHG fluxes exist at small distances on the peat plateau peatlands. From all land cover types studied the unvegetated peat circles had the highest positive radiative impact per unit area, 724 ± 282 g CO_2-eq m^{-2} y^{-1}, due to the high N_2O emissions and large net CO_2 release. There, the N_2O fluxes were responsible for 55% of the annual GHG balance as CO_2 equivalents. In contrast, the vegetated part of the peat plateau, tundra bog, represented the strongest net GHG sink on a unit area basis, -153 ± 174 g CO_2-eq m^{-2} y^{-1}. Thus, possible changes in the coverage of peat circles, affected by climate driven cryogenic processes (Chapters 4 and 5), would have implications on the total climate forcing of the peat plateaus. The same applies to the relative coverage of peat plateaus with shallow seasonal thaw depth vs. fens with deeper active layer, which is determined by permafrost distribution and, thus, climatic changes. In northern Scandinavia, the increased abundance of wetlands as a result of permafrost thaw has been already observed (Christensen et al. 2004, Johansson et al. 2006). Due to the net cooling effect of frozen peatlands and the net warming effect of unfrozen ones, the decreased permafrost coverage of high-latitude peatlands would act as a positive feedback to the climate warming.

7 *General discussion*

7.1 REGIONAL GREEN HOUSE GAS BALANCES

A recent extensive review of arctic C flux studies by McGuire et al. (2012) provides a good reference for the CO_2 and CH_4 balances of this study. In general, the review shows stronger CO_2 sink for the Northern European Arctic compared with other arctic regions, which could be explained by relatively mild climatic conditions, as discussed in Chapter 2. The growing season estimate for the CO_2 balance of the Seida study site, -127 ± 30 to -94 ± 37 g C m^{-2} (Chapter 2), is similar to the average of -94 g C m^{-2} for Northern Europe (McGuire et al. 2012), but on an annual basis Seida was a stronger sink than the North European mean (-79 ± 22 to -41 ± 57 g C m^{-2} vs. -30 g C m^{-2}). Furthermore, high summer temperatures in Seida during the study years 2007-2008 may have increased the gross CO_2 fluxes, the effect on net C balance being less clear (Parmentier et al. 2011, Lund et al. 2012).

High temperatures during peak summer likely enhanced also CH_4 release from the study region (Zhuang et al. 2004). In 2007, an increase of 8.3 ± 0.6 ppb was observed in globally averaged atmospheric CH_4 concentration. This increase could be partly attributed to anomalously high temperatures in the Arctic that lead to high emissions from arctic wetlands (Dlugokencky et al. 2009). The high temperatures directly promoted CH_4 emissions from Seida wetland sites, since they did not experience summer drought due to the floating fen surface that adjusted to the fluctuations of water level (Chapter 3). The regional CH_4 emissions were 3.5 and 5.0 g C m^{-2} for the growing season and whole year, respectively (Chapter 3), which is lower than the averages for Northern Europe (McGuire et al. 2012). A reason for this could be lower wetland coverage in Seida compared to the reference studies. Wetlands are higher CO_2 sinks and CH_4 sources than uplands (McGuire et al. 2012), and the C balance is strongly affected by the percent coverage of wet ecosystem types. In general, data from separate sites has regional meaning only if it can be put to the spatial context based on knowledge on distribution of different tundra types.

According to the only previous study on regional C balance of tundra in Northeast European Russia (Heikkinen et al. 2002, 2004), the landscape was a net C source of 35 g m^{-2} during summer season from June to September 2001. The C balance of different land cover types varied from a sink of -110 g C m^{-2} to a source of 123 g C m^{-2}. In contrast, the results of this study show significant C sink during the growing season of 91 ± 38 g C m^{-2}, ranging from -264 to 48 g C m^{-2} across the land cover types. The distribution of different land cover types in the study by Heikkinen et al. (2004) was rather similar to that of our study. However, fluxes were not measured from willow dominated stands, covering 24% of the terrain, and they were assumed to have a neutral C balance. According to the results of the present work, the willow stands actually show a very strong C sink character (Fig. 1). If the C balance of willows measured in Seida, -265 g C m^{-2} for 6 June-10 September (-295 g CO_2-C m^{-2} + 30 g CH_4-C m^{-2}), is used to recalculate the regional balance by

Heikkinen et al. (2004), it switches from a C source of 35 g m^{-2} to a C sink of -30 g m^{-2}. The contribution of willow stands on the regional CH_4 balance is even higher. Measuring CH_4 fluxes from willow stands would have likely increased the regional CH_4 emission from 1 g C m^{-2} (range -0.2-14 g C m^{-2}) estimated by Heikkinen et al. (2004). To conclude, willow stands are highly important for tundra C balance in Northeast European Russia.

The regional N_2O estimate of this study, 5.8 ± 7.1 mg N m^{-2} yr^{-1} (Chapter 6), is the first one published for tundra. The value is low due to the low coverage of the high emitting sites, peat circles, despite the large emissions on a square meter basis (growing season mean 8.1-10.3 mg N_2O m^{-2} d^{-1}; Chapter 5). According to the present understanding from Northern Finland (Chapter 5), European Russia (Chapters 4 and 5) and Siberia (Biasi et al., unpublished results), high N_2O emissions can be found from different parts of the Arctic and Subarctic but they seem to be limited to unvegetated surfaces on palsa mires and peat plateau peatlands.

7.2 SPATIAL VARIABILITY IN GREENHOUSE GAS EXCHANGE

7.2.1 Importance of different land cover types for regional carbon dioxide, methane and nitrous oxide balances

Shrub tundra heath, willows and tundra bog were the three land cover types dominating the growing season CO_2 balance: together they were responsible for almost 77% of the growing season net CO_2 sink. Shrub tundra heath and tundra bog cover a large part of the studied terrain, while willow stands are important due to their high C sink capacity per unit area (Fig. 1). The land cover types showing net C source on an annual basis - unvegetated peat circles, dry lichen tundra heath and lakes - had only minor importance to the regional CO_2 balance due to their limited distribution (Fig. 1).

The CO_2 fluxes were rather normally distributed across the land cover types (Chapter 2; Fig. 1). In contrast, clear hot spots or hot areas of CH_4 and N_2O emissions were found, while the fluxes of these gases were very small from the rest of the landscape (Fig. 1). Willow wetlands, fens and thermokarst lakes, together covering 16% of the study region, were significant CH_4 sources (Fig. 1; Chapter 3). The terrestrial CH_4 sources were responsible for 99% of the regional emission on annual basis, and the contribution of willows alone was as high as 77%, nine times their percent coverage in the landscape. The role of the CH_4 emissions from lakes in the regional scale was only marginal due to their limited distribution (~1%) and rather low emissions on a unit area basis, 3.1 g C m^{-2} yr^{-1}. It might be that we missed high emissions during the short periods of ice melt and turn-over in autumn and spring (Huttunen et al. 2004, Kankaala et al. 2006). However, we are quite sure based on our field observations that huge winter-time hot spots during the ice-cover, such as described by Walter et al. (2006), did not exist in our study lakes. None of the land cover types studied showed CH_4 uptake on an annual basis.
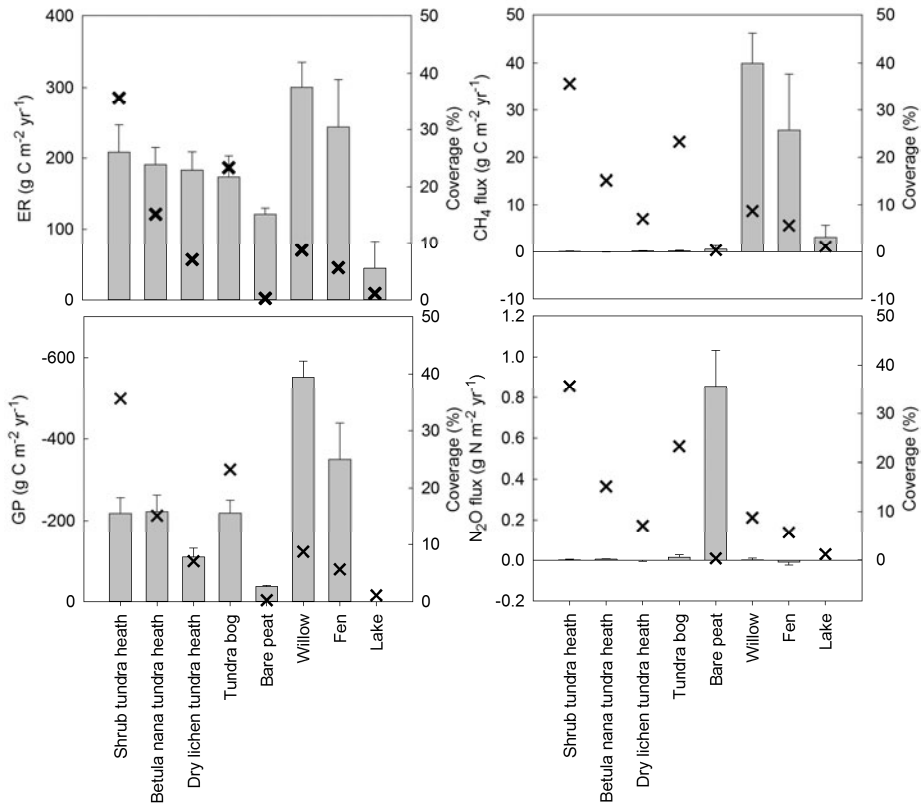
Figure 1 *Annual fluxes of CO$_2$ (ER top left, GP bottom left), CH$_4$ (top right) and N$_2$O (bottom right) of different land cover types (bars; n = 3-6) on a unit area basis vs. their percent coverage in the study area of 98.6 km^2 (crosses). Negative values indicate a GHG sink to the ecosystem, positive values indicate a GHG source to the atmosphere.*

Bare peat surfaces on peat plateaus, covering only 0.27% of the study region, were strong N$_2$O sources with summertime flux rates comparable to those commonly measured from tropical or agricultural soils (Fig. 1; Chapter 4 and 5). The unit area fluxes from the other land cover types were two to three orders of magnitude smaller than those from peat circles (Chapters 4 and 5). However, the contribution of N$_2$O emissions from tundra bog (0.01 ± 0.01 g N$_2$O-N m^{-2} yr^{-1}) to the regional N$_2$O balance is as high as 54% due to the high relative coverage in the landscape compared to peat circles (23 vs. 0.27%). Small N$_2$O uptake was regularly observed at fen surfaces, but the rates were so small that this N$_2$O sink was unimportant at the regional scale.

7.2.2 Factors explaining the spatial variability in carbon dioxide and methane fluxes

While gross photosynthesis showed ten-fold differences between the terrestrial land cover types, the variability of ecosystem respiration was only three-fold (Fig. 1). A further evidence of the role of recently fixed C as a driver of the spatial variability in the CO_2 balance is that vascular leaf area index (LAI) explained well the variability in NEE, GP and ER across all soil and vegetation types (Chapter 2). Linear correlations between LAI and CO_2 fluxes have been found also in previous studies on tundra and peatlands (Shaver et al. 2007, Street et al. 2007, Lund et al. 2010,).

Also CH_4 emission at the nine wetlands plots (willow and fen) had a strong positive correlation with LAI (Chapter 3; see also Morrissey and Livingston 1992). This can be seen as an indication of a tight link between net primary production and methanogenesis and the importance of plant-mediated CH_4 flux through plant aerenchyma (King et al. 1998, Öquist and Svensson 2002, Kutzbach et al. 2004, Ström et al. 2012). Since the studied wetlands had constantly high water table and only a thin oxidative peat layer, the CH_4 emissions were not strongly affected by CH_4 oxidation in soil. Continuously high water level and large differences in vascular plant biomass explain why water table level was unimportant in explaining the spatio-temporal variability in the wetlands studied, in contrast to many earlier reports on CH_4 fluxes in peatlands (e.g., Morrissey and Livingston 1992, Dise 1993, van Huissteden et al. 2005, Turetsky et al. 2008). The seasonal variability in CH_4 emissions was strongly driven by temperature in the anaerobic peat profile (Chapter 3). Increased evapo-transpiration expected with the warmer temperatures will probably not cause significant drying of fens in the Seida region. They are typically floating fens where the peatland surface adjusts to fluctuations of water level, and increased temperatures would likely mean increased CH_4 emissions on a unit area basis.

Due to the high explanatory power of vascular LAI for CO_2 fluxes, we were able to utilize it for the regional extrapolation of the fluxes. In Chapter 2, a regression function between LAI measured in the field and spectral information of a high resolution satellite image was used to produce a LAI map for the study region. The regional LAI derived from the map and the linear regression between LAI and CO_2 balance was used for calculating the regional CO_2 balance. The LAI-CH_4 flux dependence provided a way to explain the higher areal CH_4 flux measured by chambers than by the EC technique: the fen flux plots had higher LAI than the fen in the region on average (Chapter 3). These examples show the value of the fast, simple and non-destructive LAI measurements, and strongly suggest that LAI monitoring should be included in any CO_2 and CH_4 measurement campaign. Many previous C balance studies on tundra ecosystems do not report any estimate for vascular plant leaf area or biomass, and it can be argued that these plant variables may explain a large part of the unexplained variability between the sites. Further, LAI monitoring will be of high interest in long term studies dealing with changes in arctic ecosystems along with the climate change. Multiannual studies would reveal how much do the observed LAI-CO_2 and LAI-CH_4 dependences vary from year to year according to, e.g., climatic conditions.

7.2.3 Large nitrous oxide emissions from bare peat surfaces

Large N_2O emissions found from peat circles at the Seida study site and eroded palsa surfaces on Finnish palsa mires (Chapters 4 and 5) raise N_2O to the agenda of tundra GHG flux research. High emissions of this gas from tundra may be surprising on the background of earlier knowledge on the arctic N cycle (Section 1.3.3). However, they can be well explained by a favorable combination of biotic and abiotic factors occurring at these patches of bare peat. These factors include: i) aerobic conditions created by uplifting of the peat by permafrost, which enables sufficient mineralization of organic matter and nitrification; ii) large stocks of peat with low C:N ratio fuelling the supply of inorganic N and NO_3^-; iii) lack of vegetation that leaves the whole inorganic N pool for the soil microbes; and iv) intermediate moisture conditions allowing coupled nitrification-denitrification. Nitrate from nitrification is used as an electron acceptor in denitrification, which likely is the main pathway of N_2O production in the peat circles (Chapters 4 and 5; Palmer et al. 2012). The association between low C:N ratio and high N_2O release has been earlier shown in boreal organic soils (Klemedtsson et al. 2005). The present data from palsa mires in Finnish Lapland provide evidence that neither low C:N ratio nor lack of vegetation alone is enough to support high N_2O release - both these factors are required (Chapter 5).

Processes related to the harsh climatic conditions - frost heave, cryoturbation and wintertime wind erosion - are very important for N_2O emissions from permafrost peatlands: They create aerobic conditions in the upper peat profile, remove the vegetation cover and expose the peat with low C:N ratio to the surface (Chapter 4 and 5). Interestingly, the conditions at peat circles and eroded palsa surfaces are similar to those observed in peatlands artificially drained for economic use, known for their high N_2O emissions and high positive radiative forcing as CO_2 equivalents (Martikainen et al. 1993, Maljanen et al. 2010).

Respiration rates were high at peat circles considering lack of plants and the high age of the surface peat (3540 years; Biasi et al. 2013) and also the gross N mineralization rate was rather high (Chapter 5). Similar peat as currently found on the surface at peat circles and eroded palsas exists also in the deeper layers of permafrost peatlands. The rather high decomposability of peat plateau peat means that permafrost thawing and especially thermokarst erosion could rapidly make these deeper peat layers available for decomposition processes (see also Hugelius et al. 2012). This could lead to enhanced N and C cycling and emissions of N_2O (and CO_2/CH_4), providing that water status is favorable. Recent laboratory studies with arctic wetland soils have shown the potential of some permafrost soils for high N_2O release after permafrost thaw, drying and rewetting (Elberling et al. 2010).

The clear temperature response of N_2O emissions from peat circles (Chapter 5) would mean higher emissions in future warmer climate. Moreover, the small N_2O release occasionally observed at vegetated peat plateau surfaces in this work imply that the peat plateau as a whole has potential for N_2O release, and larger emissions might be induced by climate change. Although N_2O emissions currently have only marginal importance for the regional climate forcing, the phenomenon as such complements the understanding of N cycling in pristine northern ecosystems. There is a need for further studies investigating the mechanisms behind the N_2O emissions

and the microbial groups responsible for N transformations in the highly acidic peat.

7.3 METHODOLOGICAL CONSIDERATIONS

7.3.1 Spatial extrapolation of greenhouse gas fluxes

Due to the high overall variability in GHG fluxes across subarctic landscape and presence of hot spots, the use of high-resolution satellite data are crucial for meaningful regional extrapolation. Importance of hot spots for the total emissions of CH_4 in pristine ecosystems has been recognized also in previous studies (e.g., Bubier et al. 2005, Flessa et al. 2008). By using high resolution satellite data from a QuickBird image it was possible to catch very accurately the landscape features occurring as small patches, such as peat circles and fens, which are too small to be detected by, e.g., Landsat imagery. However, the results of this work show that in addition to the high fluxes occurring over small areas (such as CH_4 fluxes from willow) also small fluxes occurring over large areas (such as CO_2 fluxes from shrub tundra heath and *Betula nana* tundra heath and N_2O fluxes from tundra bog) matter when estimating the regional GHG balance and the net climate forcing of subarctic tundra. Accordingly, it is neither justified to limit such studies to a few land cover types that are dominant on area basis nor to concentrate on determination of accurate flux rates of the high-emitting sites only. Both are crucial for regional GHG flux assessments in tundra ecosystems and cannot be prioritized over each other.

Representative selection of measuring locations is also needed for realistic spatial extrapolation. Ecosystem types from peatlands to mineral soil and from aquatic to terrestrial sites studied at the plot scale in the present work represent 97% of the whole study region (Chapter 2). The mean growing season LAI values of the terrestrial microsites varied from 0 to 2, which covers well the variability in vascular LAI in the landscape missing only the extreme high range. According to the LAI map based on a QuickBird satellite image (resolution 2.4 m; Chapter 2), only 0.7% of the study area had a mean growing season LAI above 3, and the regional mean for the terrestrial surfaces was 0.98. A comparison of LAI at the chamber microsites and regional mean LAI of corresponding land cover types as a whole shows that the studied plots were well representative for the whole study area (Chapter 2). Vascular LAI was recognized as a factor predicting well the spatial variability in CO_2 and CH_4 fluxes (Chapters 2 and 3). Thus, there is a high confidence that the microsites selected for the study give a complete and realistic picture of the actual spatial variability across the studied terrain.

7.3.2 Comparison of chamber and eddy covariance techniques in measuring greenhouse gas fluxes in tundra

As an intermediate step in the upscaling process from the plot to the regional scale, the results of the plot scale fluxes were compared to the landscape scale CO_2 and CH_4 fluxes measured by the eddy covariance (EC) technique. The landscape composition in the EC source area, needed for area integration of the plot scale fluxes, was estimated by foot print modeling (Chapter 2). Plot scale measurements

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underestimated the gross CO_2 fluxes, but the net fluxes were in the uncertainty range of each other for the EC measuring period from late May to early October. For the growing season CO_2 balance the two measuring techniques matched very well. The plot sale measurements and the eddy covariance method agreed better on the landscape scale CH_4 emissions. This could be expected, since the spatial distribution of CH_4 emissions is much less complex than that of CO_2. Only the wet fens, willow wetlands and lakes have high CH_4 fluxes, while the emissions from the rest of the landscape are close to zero. The coverage of these land cover types was very well caught by the high-resolution QuickBird satellite image used as a basis of the land cover classification.

Since both EC and chamber methods have their advantages and disadvantages, the use of the two measuring techniques in parallel proved to be a good way to provide more sound regional flux estimates and to understand their uncertainties. Similar nested study design has been only rarely used (Soegaard et al. 2000, Zamolodchikov et al. 2003, Fox et al. 2008, Sachs et al. 2010), but can be recommended for future flux studies in order to obtain a more thorough picture of the GHG dynamics of tundra. The present work also shows that despite the criticism against the chamber method, it is very well suitable for upscaling studies in heterogeneous environments like tundra. It is the best method for studying patchy phenomena, such as the high N_2O emissions from the peat circles. Further, it allows studying the variable response of fluxes from different land cover types to environmental factors and connecting fluxes with processes.

7.4 RESPONSE OF SUBARCTIC TUNDRA TO CLIMATE CHANGE

When considering the climate change response of an ecosystem, it is important to separate the instant, short-term response from the long-term one. Short term climate response of an ecosystem appears as interannual variability, and can be thus understood by multiannual studies. For example, recently published EC time-series from the Arctic show that the current mean temperatures are optimal for the present vegetation, and during hot summer the sink character of the ecosystem can be reduced (Parmentier et al. 2011, Lund et al. 2012). Long-term changes, in turn, mean gradual adaptation of the ecosystem to the changed environmental conditions towards a new steady-state. For instance, a continuous positive trend in summer temperatures with more frequent hot summers would cause gradual changes in plant community composition when the ecosystem would slowly adapt to the new average conditions (e.g., Chapin et al. 1995). Based on an annual/biannual study like this one, there are only limited possibilities to predict the response of ecosystem to climate change. Nevertheless, some interpretations can still be made based on the GHG exchange at present.

In our study we observed a linear response of NEE to increased LAI (Chapter 2), meaning that better growth of vascular plants due to warming could lead to increased C sink to the studied tundra ecosystem. Here, the response of C balance is likely different in wetlands, where soil C is conserved by constantly high water tables (Chapter 3), and at drier land cover types with aerobic soils. The trend of

increased willow growth related to warming has been already observed during the last decades in Northeast European Russia (Forbes et al. 2010). In our study the willow stands were shown to be very important for the regional CO_2 and CH_4 balances and their importance will likely increase in the future. On upland tundra heath, the increased air and soil temperatures might in turn threaten the CO_2 sink character by increasing respiration (this study; Zamolodchikov et al. 2000, Heikkinen et al. 2004). Since upland tundra heath covers a large part of the study region, the changes in its GHG dynamics will impact significantly the regional C balance.

Integrative studies that combine process understanding with flux observation and incorporation of this knowledge into carbon-climate models have been suggested as a means for reducing the large uncertainty in the response of tundra C balance to climate change (McGuire et al. 2009). This kind of work is currently in progress with the Seida flux data. However, presence of permafrost adds complexity to model predictions since it is extremely difficult to predict the landscape change in future in permafrost affected terrain. Although increased coverage of wetlands at the expense of drier permafrost peatlands due to melting of permafrost has been reported from North Scandinavia and Canada (Luoto et al. 2004, Payette et al. 2004, Johansson et al. 2006), the thaw can in some cases lead to the opposite. At least for lake ecosystems drying due to enhanced subsurface water-flow following permafrost thaw has been reported (Smith et al. 2005, Jones et al. 2011). The redox conditions are very important for GHG release after permafrost thaw: For instance, C loss was 3.9 to 10 times higher in aerobic than in anaerobic conditions in thawed permafrost soils in a study by Lee et al. (2012). Similarly, Elberling et al. (2010) recognized in their incubation study the importance of drainage conditions following permafrost thaw for N_2O release from arctic soils.

Due to the contrasting GHG fluxes of different land cover types, e.g., peat plateaus with shallow active layer vs. fens with deeper seasonal thaw (Chapter 6), the changes in landscape composition will have a strong effect on the GHG balance and net radiative impact of tundra. For CH_4, increased fen coverage would mean higher emissions in the landscape scale (Chapter 3). The peat plateau coverage relative to wet fens is also crucial for the regional N_2O emissions that occur exclusively on peat plateaus. In the long term, the changes in the landscape structure will likely overrule the (more rapid) changes that will happen in the unit area fluxes of different land cover types.

7.5 SUMMARY AND CONCLUSIONS

In the following, the key findings of the study are listed:

- **Green house gas fluxes of subarctic tundra show large spatial variability in the scale of meters**. Especially for methane (CH_4) and nitrous oxide (N_2O), hot spots are important. Therefore, high resolution spatial data on fluxes and landscape composition are essential for producing realistic flux estimates in regional scale.

- **Spatial variability in carbon dioxide (CO_2) fluxes and in wetland CH_4 emissions is well explained by the leaf area index of vascular plants.** This is an easily measurable variable and can be related to remote sensing data, meaning good perspectives from the upscaling point of view.

- **Subarctic permafrost peatlands have unvegetated surfaces that, in contrast to pristine arctic soils in general, release N_2O in high amounts.** These bare peat surfaces are formed by natural processes related to the harsh climate: frost-action and wind abrasion. Sufficient drainage, a low carbon to nitrogen ratio and the absence of vegetation were identified as prerequisites for high N_2O emissions.

- **Eddy covariance and chamber techniques give similar areal green house gas exchange** in subarctic tundra, offering together with remote sensing data the possibility to upscale the chamber fluxes to the regional level.

- **The long-term climate change response of subarctic tundra will be determined by changes in the coverage of different land-cover types.** Here, one of the key factors will be permafrost distribution in peatlands that determines the relative coverage of peat plateaus vs. wet peatlands. These peatland types have contrasting fluxes with respect to all of the three green house gases.

References

AMAP. 2011. Executive summary and key messages. In: Snow, Water, Ice and Permafrost in the Arctic (SWIPA): Climate Change and the Cryosphere. Arctic Monitoring and Assessment Programme (AMAP): Oslo, Norway. pp. vi-xii.

Anisimov O and Reneva S. 2006. Permafrost and changing climate: the Russian perspective. *Ambio* **35:** 169-175.

Arens SJT, Sullivan PF and Welker JM. 2008. Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem. *J Geophys Res-Biogeo* **113:** G03S09. doi: 10.1029/2007JG000508.

Aurela M, Laurila T and Tuovinen J. 2002. Annual CO_2 balance of a subarctic fen in northern Europe: Importance of the wintertime efflux. *J Geophys Res-Atmos* **107:** 4607. doi: 10.1029/2002JD002055.

Aurela M, Laurila T and Tuovinen J. 2004. The timing of snow melt controls the annual CO_2 balance in a subarctic fen. *Geophys Res Lett* **31:** L16119. doi: 10.1029/2004GL020315.

Bäckstrand K, Crill PM, Jackowicz-Korczyñski M, Mastepanov M, Christensen TR and Bastviken D. 2010. Annual carbon gas budget for a subarctic peatland, Northern Sweden. *Biogeosciences* **7:** 95-108.

Bastviken D, Tranvik LJ, Downing JA, Crill PM and Enrich-Prast A. 2011. Freshwater methane emissions offset the continental carbon sink. *Science* **331:** 50.

Bazilevich NI. 1993. Biological Productivity of Ecosystems of Northern Eurasia. Nauka: Moscow, Russia. pp. 293.

Biasi C, Jokinen S, Marushchak ME, Hämäläinen K, Trubnikova T, Oinonen M and Martikainen PJ. 2013. Microbial respiration in arctic upland and peat soils as a source of atmospheric carbon dioxide. *Ecosystems*. doi: 10.1007/s10021-013-9710-z.

Blodau C, Rees R, Flessa H, Rodionov A, Guggenberger G, Knorr K, Shibistova O, Zrazhevskaya G, Mikheeva N and Kasansky OA. 2008. A snapshot of CO_2 and CH_4 evolution in a thermokarst pond near Igarka, northern Siberia. *J Geophys Res-Biogeo* **113:** G03023. doi: 10.1029/2007JG000652.

Bockheim JG. 2007. Importance of cryoturbation in redistributing organic carbon in permafrost-affected soils. *Soil Sci Soc Am J* **71:** 1335-1342. doi: 10.2136/sssaj2006.0414N.

Bockheim JG and Tarnocai C. 1998. Recognition of cryoturbation for classifying permafrost-affected soils. *Geoderma* **81:** 281-293.

Brummell ME, Farrell RE and Siciliano SD. 2012. Greenhouse gas soil production and surface fluxes at a high arctic polar oasis. *Soil Biol Biochem* **52:** 1-12. doi: 10.1016/j.soilbio.2012.03.019.

Bubier J, Crill P and Mosedale A. 2002. Net ecosystem CO_2 exchange measured by autochambers during the snow-covered season at a temperate peatland. *Hydrol Process* **16:** 3667-3682. doi: 10.1002/hyp.1233.

Bubier J, Moore T, Savage K and Crill P. 2005. A comparison of methane flux in a boreal landscape between a dry and a wet year. *Global Biogeochem Cy* **19:** GB1023. doi: 10.1029/2004GB002351.

Butterbach-Bahl K, Kock M, Willibald G, Hewett B, Buhagiar S, Papen H and Kiese R. 2004. Temporal variations of fluxes of NO, NO_2, N_2O, CO_2, and CH_4 in a tropical rain forest ecosystem. *Global Biogeochem Cy* **18:** GB3012. doi: 10.1029/2004GB002243.

Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ and Laundre JA. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* **76:** 694-711.

Christensen TR, Johansson T, Aakerman HJ, Mastepanov M, Malmer N, Friborg T, Crill P and Svensson BH. 2004. Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. *Geophys Res Lett* **31:** . doi: 10.1029/2003GL018680.

Christensen TR, Michelsen A and Jonasson S. 1999. Exchange of CH_4 and N_2O in a subarctic heath soil: effects of inorganic N and P and amino acid addition. *Soil Biol Biochem* **31:** 637-641.

Christensen T, Friborg T, Sommerkorn M, Kaplan J, Illeris L, Soegaard H, Nordstroem C and Jonasson S. 2000. Trace gas exchange in a high-arctic valley 1. Variations in CO_2 and CH_4 flux between tundra vegetation types. *Global Biogeochem Cy* **14:** 701-713. doi: 10.1029/1999GB001134.

Christensen T, Michelsen A, Jonasson S and Schmidt I. 1997. Carbon dioxide and methane exchange of a subarctic heath in response to climate change related environmental manipulations. *Oikos* **79:** 34-44. doi: 10.2307/3546087.

Corradi C, Kolle O, Walter K, Zimov SA and Schulze E-D. 2005. Carbon dioxide and methane exchange of a north-east Siberian tussock tundra. *Global Change Biol* **11:** 1910-1925. doi: 10.1111/j.1365-2486.2005.01023.x.

Dentener, FJ 2006. Global maps of atmospheric nitrogen deposition, 1860, 1993, and 2050., doi: 10.3334/ORNLDAAC/830.

Desyatkin AR, Takakai F, Fedorov PP, Nikolaeva MC, Desyatkin RV and Hatano R. 2009. CH_4 emission from different stages of thermokarst formation in Central Yakutia, East Siberia. *Soil Sci Plant Nutr* **55:** 558-570. doi: 10.1111/j.1747-0765.2009.00389.x.

Dise NB. 1993. Methane emission from Minnesota peatlands: spatial and seasonal variability. *Global Biogeochem Cy* **7:** 123-142.

Dlugokencky EJ, Bruhwiler L, White JWC, Emmons LK, Novelli PC, Montzka A, Masarie KA, Lang PM, Crotwell AM, Miller JB and Gatti LV. 2009. Observational constraints on recent increases in the atmospheric CH_4 burden. *Geophys Res Lett* **36**: L18803. doi:10.1029/2009GL039780.

Dorrepaal E, Toet S, van Logtestijn RSP, Swart E, van de Weg MJ, Callaghan TV and Aerts R. 2009. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* **460:** 616-619. doi: 10.1038/nature08216.

Elberling B, Christiansen HH and Hansen BU. 2010. High nitrous oxide production from thawing permafrost. *Nat Geosci* **3:** 332-335. doi: 10.1038/ngeo893.

Fan S, Wofsy S, Bakwin P, Jacob D, Anderson S, Kebabian P, McManus J, Kolb C and Fitzjarrald D. 1992. Micrometeorological measurements of CH_4 and CO_2 exchange between the atmosphere and sub-arctic tundra. *J Geophys Res-Atmos* **97:** 16627-16643.

Flessa H, Rodionov A, Guggenberger G, Fuchs H, Magdon P, Shibistova O, Zrazhevskaya G, Mikheyeva N, Kasansky OA and Blodau C. 2008. Landscape controls of CH_4 fluxes in a catchment of the forest tundra ecotone in northern Siberia. *Global Change Biol* **14:** 2040-2056. doi: 10.1111/j.1365-2486.2008.01633.x.

Forbes BC, Macias Fauria M and Zetterberg P. 2010. Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biol* **16:** 1542-1554. doi: 10.1111/j.1365-2486.2009.02047.x.

Fox AM, Huntley B, Lloyd CR, Williams M and Baxter R. 2008. Net ecosystem exchange over heterogeneous Arctic tundra: Scaling between chamber and eddy covariance measurements. *Global Biogeochem Cy* **22:** GB2027. doi: 10.1029/2007GB003027.

French HM. 2007. The Periglacial Environment, Third edition. John Wiley & Sons Ltd: Chichester, UK. pp. 458.

Friborg T, Soegaard H, Christensen TR, Lloyd CR and Panikov NS. 2003. Siberian wetlands: Where a sink is a source. *Geophys Res Lett* **30:** . doi: 10.1029/2003GL017797.

Frolking S, Roulet N and Fuglestvedt J. 2006. How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *J Geophys Res-Biogeo* **111:** G01008. doi: 10.1029/2005JG000091.

Gregorich EG, Hopkins DW, Elberling B, Sparrow AD, Novis P, Greenfield LG and Rochette P. 2006. Emission of CO_2, CH_4 and N_2O from lakeshore soils in an Antarctic dry valley. *Soil Biol Biochem* **38:** 3120-3129. doi: 10.1016/j.soilbio.2006.01.015.

Groendahl L, Friborg T and Soegaard H. 2007. Temperature and snow-melt controls on interannual variability in carbon exchange in the high Arctic. *Theor Appl Climatol* **88:** 111-125. doi: 10.1007/s00704-005-0228-y.

Hao W, Scharffe D, Crutzen P and Sanhueza E. 1988. Production of N_2O, CH_4, and CO_2 from soils in the tropical savanna during the dry deason. *J Atmos Chem* **7:** 93-105. doi: 10.1007/BF00048256.

Heikkinen JEP, Elsakov V and Martikainen PJ. 2002. Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia. *Global Biogeochem Cy* **16:** 1115. doi: 10.1029/2002GB001930.

Heikkinen JEP, Virtanen T, Huttunen JT, Elsakov V and Martikainen PJ. 2004. Carbon balance in East European tundra. *Global Biogeochem Cy* **18:** GB1023.

Hugelius G, Virtanen T, Kaverin D, Pastukhov A, Rivkin F, Marchenko S, Romanovsky V and Kuhry P. 2011. High-resolution mapping of ecosystem carbon storage and potential effects of permafrost thaw in periglacial terrain, European Russian Arctic. *J Geophys Res-Biogeo* **116:** G03024. doi: 10.1029/2010JG001606.

Hugelius G, Routh J, Kuhry P and Crill P. 2012. Mapping the degree of decomposition and thaw remobilization potential of soil organic matter in discontinuous permafrost terrain. J Geophys Res-Biogeosci 117: G02030. doi: 10.1029/2011JG001873.

Humphreys ER and Lafleur PM. 2011. Does earlier snowmelt lead to greater CO_2 sequestration in two low Arctic tundra ecosystems?. *Geophys Res Lett* **38:** L09703. doi: 10.1029/2011GL047339.

Huttunen JT, Lappalainen KM, Saarijärvi E, Väsänen T and Martikainen PJ. 2001. A novel sediment gas sampler and a subsurface gas collector used for measurement of the ebullition of methane and carbon dioxide from a eutrophied lake. *Sci Total Environ* **266:** 153-158.

Huttunen J, Hammar T, Manninen P, Servomaa K and Martikainen P. 2004. Potential springtime greenhouse gas emissions from a small southern boreal lake (Keihasjarvi, Finland). *Boral Environ Res* **9:** 421-427.

IPCC. 1990. Chapter 2: Radiative forcing of climate. In: Houghton JT, Jenkins GJ and Ephraums JJ. Climate Change: The IPCC Scientific Assessment. Cambridge University Press: Cambridge, UK, New York, NY, USA and Melbourne, Australia. pp. 41-68.

IPCC. 2007. Chapter 2: Changes in atmospheric constituents and in radiative forcing. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M and Miller HL. Climate Change 2007: The Physical Science Basis. Cambridge University Press: Cambridge, United Kingdom and New York, NY, USA. pp. 129-234.

Jackowicz-Korczynski M, Christensen TR, Backstrand K, Crill P, Friborg T, Mastepanov M and Strom L. 2010. Annual cycle of methane emission from a subarctic peatland. *J Geophys Res-Biogeo* **115:** G02009. doi: 10.1029/2008JG000913.

Johansson T, Malmer N, Crill PM, Friborg T, Akerman JH, Mastepanov M and Christensen TR. 2006. Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biol* **12:** 2352-2369. doi: 10.1111/j.1365-2486.2006.01267.x.

Johnson L, Shaver G, Cades D, Rastetter E, Nadelhoffer K, Giblin A, Laundre J and Stanley A. 2000. Plant carbon-nutrient interactions control CO_2 exchange in Alaskan wet sedge tundra ecosystems. *Ecology* **81:** 453-469. doi: 10.1890/0012-9658(2000)081[0453:PCNICC]2.0.CO;2.

Jonasson S, Michelsen A, Schmidt I and Nielsen E. 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology* **80:** 1828-1843. doi: 10.1890/0012-9658(1999)080[1828:RIMAPT]2.0.CO;2.

Jones BM, Grosse G, Arp CD, Jones MC, Anthony KMW and Romanovsky VE. 2011. Modern thermokarst lake dynamics in the continuous permafrost zone, northern Seward Peninsula, Alaska. *J Geophys Res-Biogeo* **116:** G00M03. doi: 10.1029/2011JG001666.

Kaiser C, Meyer H, Biasi C, Rusalimova O, Barsukov P and Richter A. 2007. Conservation of soil organic matter through cryoturbation in arctic soils in Siberia. *J Geophys Res-Biogeo* **112:** G02017. doi: 10.1029/2006JG000258.

Kankaala P, Huotari J, Peltomaa E, Saloranta T and Ojala A. 2006. Methanotrophic activity in relation to methane efflux and total heterotrophic bacterial production in a stratified, humic, boreal lake. *Limnol Oceanogr* **51:** 1195-1204.

Kattsov, VM et al. 2005. Chapter 4: Future climate change: Modeling and scenarios for the arctic. In: Symon C, Arris L and Heal B. Arctic Climate Impact Assessment. Cambridge University Press: New York, NY, USA. pp. 99-150.

King JY, Reeburgh WS and Regli SK. 1998. Methane emission and transport by Arctic sedges in Alaska: Results of a vegetation removal experiment. *J Geophys Res-Atmos* **103:** 29,083-29,092.

Klemedtsson L, von Arnold K, Weslien P and Gundersen P. 2005. Soil CN ratio as a scalar parameter to predict nitrous oxide emissions. *Global Change Biol* **11:** 1142-1147. doi: 10.1111/j.1365-2486.2005.00973.x.

Kling GW, Kipphut GW and Miller MC. 1991. Arctic lakes and streams as gas conduits to the atmosphrere:Implications for tundra carbon budgets. *Science* **251:** 298-301.

Kling G, Kipphut G and Miller M. 1992. The flux of CO_2 and CH_4 from lakes and rivers in Arctic Alaska. *Hydrobiologia* **240:** 23-36. doi: 10.1007/BF00013449.

Kutzbach L, Wagner D and Pfeiffer EM. 2004. Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry* **69:** 341-362.

Lafleur PM and Humphreys ER. 2008. Spring warming and carbon dioxide exchange over low Arctic tundra in central Canada. *Global Change Biol* **14:** 740-756. doi: 10.1111/j.1365-2486.2007.01529.x.

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Laidler GJ and Treitz P. 2003. Biophysical remote sensing of arctic environments. *Prog Phys Geog* **27:** 44-68. doi: 10.1191/0309133303pp358ra.

Laurila T, Soegaard H, Lloyd CR, Aurela M, Tuovinen JP and Nordstroem C. 2001. Seasonal variations of net CO_2 exchange in European Arctic ecosystems. *Theor Appl Climatol* **70:** 183-201.

Lee H, Schuur EAG, Inglett KS, Lavoie M and Chanton JP. 2012. The rate of permafrost carbon release under aerobic and anaerobic conditions and its potential effects on climate. *Global Change Biol* **18:** 515-527. doi: 10.1111/j.1365-2486.2011.02519.x.

Lee H, Schuur EG, Vogel JG, Lavoie M, Bhadra D and Staudhammer CL. 2011. A spatially explicit analysis to extrapolate carbon fluxes in upland tundra where permafrost is thawing. *Global Change Biol* **17:** 1379-1393. doi: 10.1111/j.1365-2486.2010.02287.x.

Liss PS and Slater PG. 1974. Flux of gases across the air-sea interface. *Nature* **247:** 181-184.

Ludwig B, Teepe R, de Gerenyu VL and Flessa H. 2006. CO_2 and N_2O emissions from gleyic soils in the Russian tundra and a German forest during freeze-thaw periods - a microcosm study. *Soil Biol Biochem* **38:** 3516-3519.

Lund M, Falk JM, Friborg T, Mbufong HN, Sigsgaard C, Soegaard H and Tamstorf MP. 2012. Trends in CO_2 exchange in a high Arctic tundra heath, 2000-2010. *J Geophys Res-Biogeo* **117:** G02001. doi: 10.1029/2011JG001901.

Lund M et al. 2010. Variability in exchange of CO_2 across 12 northern peatland and tundra sites. *Global Change Biol* **16:** 2436-2448. doi: 10.1111/j.1365-2486.2009.02104.x.

Luo GJ, Brueggemann N, Wolf B, Gasche R, Grote R and Butterbach-Bahl K. 2012. Decadal variability of soil CO_2, NO, N_2O, and CH_4 fluxes at the Hoglwald Forest, Germany. *Biogeosciences* **9:** 1741-1763. doi: 10.5194/bg-9-1741-2012.

Luoto M, Heikkinen RK and Carter TR. 2004. Loss of palsa mires in Europe and biological consequences. *Environ. Conserv.* **31:** 30-37. doi: 10.1017/S0376892904001018.

Ma WK, Schautz A, Fishback LE, Bedard-Haughn A, Farrell RE and Siciliano SD. 2007. Assessing the potential of ammonia oxidizing bacteria to produce nitrous oxide in soils of a high arctic lowland ecosystem on Devon Island, Canada. *Soil Biol Biochem* **39:** 2001-2013. doi: 10.1016/j.soilbio.2007.03.001.

Maljanen M, Liikanen A, Silvola J and Martikainen P. 2003. Measuring N_2O emissions from organic soils by closed chamber or soil/snow N_2O gradient methods. *Eur J Soil Sci* **54:** 625-631. doi: 10.1046/j.1365-2389.2003.00531.x.

Maljanen M, Sigurdsson BD, Guðmundsson J, Óskarsson H, Huttunen JT and Martikainen PJ. 2010. Greenhouse gas balances of managed peatlands in the Nordic countries – present knowledge and gaps. *Biogeosciences* **7:** 2711-2738. doi: 10.5194/bg-7-2711-2010.

Maljanen M, Virkajärvi P, Hytönen J, Öquist M, Sparrman T and Martikainen PJ. 2009. Nitrous oxide production in boreal soils with variable organic matter content at low temperature - snow manipulation experiment. *Biogeosciences* **6:** 2461-2473.

Martikainen PJ, Nykänen H, Crill P and Silvola J. 1993. Effect of a Lowered Water-Table on Nitrous-Oxide Fluxes from Northern Peatlands. *Nature* **366:** 51-53.

Mastepanov M, Sigsgaard C, Dlugokencky EJ, Houweling S, Strom L, Tamstorf MP and Christensen TR. 2008. Large tundra methane burst during onset of freezing. *Nature* **456:** 628-U58. doi: 10.1038/nature07464.

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McGuire AD et al. 2012. An assessment of the carbon balance of Arctic tundra: comparisons among observations, process models, and atmospheric inversions. *Biogeosciences* **9:** 3185-3204. doi: 10.5194/bg-9-3185-2012.

McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW and Roulet N. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecol Monogr* **79:** 523-555. doi: 10.1890/08-2025.1.

Moncrieff J, Massheder J, deBruin H, Elbers J, Friborg T, Heusinkveld B, Kabat P, Scott S, Soegaard H and Verhoef A. 1997. A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *J Hydrol* **189:** 589-611.

Morrissey L and Livingston G. 1992. Methane emissions from Alaska Arctic tundra - an assessment of local spatial variability. *J Geophys Res-Atmos* **97:** 16661-16670.

Nadelhoffer KJ, Giblin AE, Shaver GR and Laundre JA. 1991. Effects of temperature and substrate quality on element mineralization in 6 arctic soils. *Ecology* **72:** 242-253.

Natali SM, Schuur EAG, Trucco C, Pries CEH, Crummer KG and Lopez AFB. 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Global Change Biol* **17:** 1394-1407. doi: 10.1111/j.1365-2486.2010.02303.x.

Nordstroem C, Soegaard H, Christensen TR, Friborg T and Hansen BU. 2001. Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in NE-Greenland. *Theor Appl Climatol* **70:** 149-149-166.

Nykänen H, Heikkinen JEP, Pirinen L, Tiilikainen K and Martikainen PJ. 2003. Annual CO_2 exchange and CH_4 fluxes on a subarctic palsa mire during climatically different years. *Global Biogeochem Cy* **17:** 1018. doi: 10.1029/2002GB001861.

Oberman N. 2008. Contemporary permafrost degradation of northern European Russia. Paper presented at Ninth International Conference on Permafrost, Univ. of Alaska Fairbanks, Fairbanks, Alaska, 29 June to 3 July.

Oechel W et al. 2000. A scaling approach for quantifying the net CO_2 flux of the Kuparuk River Basin, Alaska. *Global Change Biol* **6:** 160-173. doi: 10.1046/j.1365-2486.2000.06018.x.

Oksanen PO, Kuhry P and Alekseeva RN. 2001. Holocene development of the Rogovaya River peat plateau, European Russian Arctic. *Holocene* **11:** 25-40.

Öquist M and Svensson B. 2002. Vascular plants as regulators of methane emissions from a subarctic mire ecosystem. *J Geophys Res-Atmos* **107:** 4580. doi: 10.1029/2001JD001030.

Oremland R and Culbertson C. 1992. Importance of methane-oxidizing bacteria in the methane budget as revealed by the use of a specific inhibitor. *Nature* **356:** 421-423. doi: 10.1038/356421a0.

Palmer K, Biasi C and Horn MA. 2012. Contrasting denitrifier communities relate to contrasting N_2O emission patterns from acidic peat soils in arctic tundra. *ISME J* **6:** 1058-1077. doi: 10.1038/ismej.2011.172.

Parmentier FJW, van der Molen MK, van Huissteden J, Karsanaev SA, Kononov AV, Suzdalov DA, Maximov TC and Dolman AJ. 2011. Longer growing seasons do not increase net carbon uptake in the northeastern Siberian tundra. *J Geophys Res-Biogeo* **116:** G04013. doi: 10.1029/2011JG001653.

Payette S, Delwaide A, Caccianiga M and Beauchemin M. 2004. Accelerated thawing of subarctic peatland permafrost over the last 50 years. *Geophys. Res. Lett.* **31:** L18208. doi: 10.1029/2004GL020358.

Post WM, Pastor J, Zinke PJ and Stangenberger AG. 1985. Global patterns of soil nitrogen storage. *Nature* **317:** 613-616.

Qian H, Joseph R and Zeng N. 2010. Enhanced terrestrial carbon uptake in the Northern High Latitudes in the 21st century from the Coupled Carbon Cycle Climate Model Intercomparison Project model projections. *Global Change Biol* **16:** 641-656. doi: 10.1111/j.1365-2486.2009.01989.x.

Reeburgh WS, King JY, Regli SK, Kling GW, Auerbach NA and Walker DA. 1998. A CH_4 emission estimate for the Kuparuk River basin, Alaska. *J Geophys Res-Atmos* **103:** 29,005-29,013.

Regina K, Nykänen H, Silvola J and Martikainen PJ. 1996. Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. *Biogeochemistry* **35:** 401-418.

Rennermalm A, Soegaard H and Nordstroem C. 2005. Interannual variability in carbon dioxide exchange from a high arctic fen estimated by measurements and modeling. *Arct Antarct Alp Res* **37:** 545-556. doi: 10.1657/1523-0430(2005)037[0545:IVICDE]2.0.CO;2.

Repo ME, Huttunen JT, Naumov AV, Chichulin AV, Lapshina ED, Bleuten W and Martikainen PJ. 2007. Release of CO_2 and CH_4 from small wetland lakes in western Siberia. *Tellus B* **59:** 788-796. doi: 10.1111/j.1600-0889.2007.00301.x.

Richardson D, Felgate H, Watmough N, Thomson A and Baggs E. 2009. Mitigating release of the potent greenhouse gas N_2O from the nitrogen cycle - could enzymic regulation hold the key?. *Trends Biotechnol* **27:** 388-397. doi: 10.1016/j.tibtech.2009.03.009.

Riordan B, Verbyla D and McGuire AD. 2006. Shrinking ponds in subarctic Alaska based on 1950-2002 remotely sensed images. *J Geophys Res-Biogeo* **111:** G04002. doi: 10.1029/2005JG000150.

Rodionow A, Flessa H, Kazansky O and Guggenberger G. 2006. Organic matter composition and potential trace gas production of permafrost soils in the forest tundra in northern Siberia. *Geoderma* **135:** 49-62.

Sachs T, Giebels M, Boike J and Kutzbach L. 2010. Environmental controls on CH_4 emission from polygonal tundra on the microsite scale in the Lena river delta, Siberia. *Global Change Biol* **16:** 3096-3110. doi: 10.1111/j.1365-2486.2010.02232.x.

Sachs T, Wille C, Boike J and Kutzbach L. 2008. Environmental controls on ecosystem-scale CH_4 emission from polygonal tundra in the Lena River Delta, Siberia. *J Geophys Res-Biogeo* **113:** G00A03. doi: 10.1029/2007JG000505.

Sannel ABK and Kuhry P. 2009. Holocene peat growth and decay dynamics in sub-arctic peat plateaus, west-central Canada. *Boreas* **38:** 13-24. doi: 10.1111/j.1502-3885.2008.00048.x.

Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO and Osterkamp TE. 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* **459:** 556-559. doi: 10.1038/nature08031.

Seppälä M. 2003. Surface abrasion of palsas by wind action in Finnish Lapland. *Geomorphology* **52:** 141-148. doi: 10.1016/S0169-555X(02)00254-4.

Shaver GR, Street LE, Rastetter EB, Van Wijk MT and Williams M. 2007. Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. *J Ecol* **95:** 802-817. doi: 10.1111/j.1365-2745.2007.01259.x.

Shaver G, Bret-Harte S, Jones M, Johnstone J, Gough L, Laundre J and Chapin F. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* **82:** 3163-3181. doi: 10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2.

Shaver G and Chapin F. 1995. Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography* **18:** 259-275. doi: 10.1111/j.1600-0587.1995.tb00129.x.

Shaver G, Johnson L, Cades D, Murray G, Laundre J, Rastetter E, Nadelhoffer K and Giblin A. 1998. Biomass and CO_2 flux in wet sedge tundras: Responses to nutrients, temperature, and light. *Ecol Monogr* **68:** 75-97. doi: 10.2307/2657144.

Siciliano SD, Ma WK, Ferguson S and Farrell RE. 2009. Nitrifier dominance of Arctic soil nitrous oxide emissions arises due to fungal competition with denitrifiers for nitrate. *Soil Biol Biochem* **41:** 1104-1110. doi: 10.1016/j.soilbio.2009.02.024.

Sjögersten S and Wookey P. 2002. Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra ecotone in the Fennoscandian mountains. *Global Change Biol* **8:** 885-894. doi: 10.1046/j.1365-2486.2002.00522.x.

Smith L, Sheng Y, MacDonald G and Hinzman L. 2005. Disappearing Arctic lakes. *Science* **308:** 1429-1429. doi: 10.1126/science.1108142.

Soegaard H, Nordstroem C, Friborg T, Hansen BU, Christensen TR and Bay C. 2000. Trace gas exchange in a high-arctic valley. 3. Integrating and scaling CO_2 fluxes from canopy to landscape using flux data, footprint modeling, and remote sensing. *Global Biogeochem Cy* **14:** 725-744.

Sommerfeld RA, Mosier AR and Musselman RC. 1993. CO_2, CH_4 and N_2O Flux through a Wyoming Snowpack and Implications for Global Budgets. *Nature* **361:** 140-142.

Soussana JF et al. 2007. Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. *Agr Ecosyst Environ* **121:** 121-134. doi: 10.1016/j.agee.2006.12.022.

Stewart KJ, Brummell ME, Farrell RE and Siciliano SD. 2012. N_2O flux from plant-soil systems in polar deserts switch between sources and sinks under different light conditions. *Soil Biol Biochem* **48:** 69-77. doi: 10.1016/j.soilbio.2012.01.016.

Stoy PC, Williams M, Disney M, Prieto-Blanco A, Huntley B, Baxter R and Lewis P. 2009. Upscaling as ecological information transfer: a simple framework with application to Arctic ecosystem carbon exchange. *Landscape Ecol* **24:** 971-986. doi: 10.1007/s10980-009-9367-3.

Street LE, Shaver GR, Williams M and Van Wijk MT. 2007. What is the relationship between changes in canopy leaf area and changes in photosynthetic CO_2 flux in arctic ecosystems?. *J Ecol* **95:** 139-150. doi: 10.1111/j.1365-2745.2006.01187.x.

Ström L, Tagesson T, Mastepanov M and Christensen TR. 2012. Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. *Soil Biol Biochem* **45:** 61-70. doi: 10.1016/j.soilbio.2011.09.005.

Sturm M, McFadden J, Liston G, Chapin F, Racine C and Holmgren J. 2001. Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. *J Climate* **14:** 336-344. doi: 10.1175/1520-0442(2001)014<0336:SSIIAT>2.0.CO;2.

Takakai F, Desyatkin AR, Lopez CML, Fedorov AN, Desyatkin RV and Hatano R. 2008. CH_4 and N_2O emissions from a forest-alas ecosystem in the permafrost taiga forest region, eastern Siberia, Russia. *J Geophys Res-Biogeo* **113:** G02002. doi: 10.1029/2007JG000521.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G and Zimov S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem Cy* **23:** GB2023. doi: 10.1029/2008GB003327.

Trucco C, Schuur EAG, Natali SM, Belshe EF, Bracho R and Vogel J. 2012. Seven-year trends of CO_2 exchange in a tundra ecosystem affected by long-term permafrost thaw. *J Geophys Res-Biogeo* **117:** G02031. doi: 10.1029/2011JG001907.

Turetsky MR, Treat CC, Waldrop MP, Waddington JM, Harden JW and McGuire AD. 2008. Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *J Geophys Res-Biogeo* **113:** G00A10. doi: 10.1029/2007JG000496.

van Huissteden J, Maximov TC and Dolman AJ. 2005. High methane flux from an arctic floodplain (Indigirka lowlands, eastern Siberia). *J Geophys Res-Biogeo* **110:** Art. No. G02002. doi: 10.1029/2005JG000010.

van Huissteden J, Berrittella C, Parmentier FJW, Mi Y, Maximov TC and Dolman AJ. 2011. Methane emissions from permafrost thaw lakes limited by lake drainage. *Nature Clim Change* **1:** 119-123. doi: 10.1038/NCLIMATE1101.

Vogel J, Schuur EAG, Trucco C and Lee H. 2009. Response of CO_2 exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development. *J Geophys Res-Biogeo* **114:** G04018. doi: 10.1029/2008JG000901.

Wagner D, Kobabe S, Pfeiffer E and Hubberten H. 2003. Microbial controls on methane fluxes from a polygonal tundra of the Lena Delta, Siberia. *Permafrost Periglac* **14:** 173-185. doi: 10.1002/ppp.443.

Walter KM, Zimov SA, Chanton JP, Verbyla D and Chapin,F.S.,,III. 2006. Methane bubbling from Siberian thaw lakes as a positive feedback to climate warming. *Nature* **443:** 71-75. doi: 10.1038/nature05040.

Whalen SC. 2005. Biogeochemistry of methane exchange between natural wetlands and the atmosphere. *Environ Eng Sci* **22:** 73-94.

Wille C, Kutzbach L, Sachs T, Wagner D and Pfeiffer E. 2008. Methane emission from Siberian arctic polygonal tundra: eddy covariance measurements and modeling. *Global Change Biol* **14:** 1395-1408. doi: 10.1111/j.1365-2486.2008.01586.x.

Zamolodchikov D, Karelin D and Ivaschenko A. 2000. Sensitivity of tundra carbon balance to ambient temperature. *Water Air Soil Poll* **119:** 157-169.

Zamolodchikov DG, Karelin DV, Ivaschenko AI, Oechel WC and Hastings SJ. 2003. CO_2 flux measurements in Russian Far East tundra using eddy covariance and closed chamber techniques. *Tellus B* **55:** 879-892.

Zhuang Q, Melillo J, Kicklighter D, Prinn R, McGuire A, Steudler P, Felzer B and Hu S. 2004. Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: A retrospective analysis with a process-based biogeochemistry model. *Global Biogeochem Cy* **18:** GB3010. doi: 10.1029/2004GB002239.

Zimov SA, Voropaev YV, Semiletov IP, Davidov SP, Prosiannikov SF, Chapin FS,III, Chapin MC, Trumbore S and Tyler S. 1997. North Siberian lakes: A methane source fueled by Pleistocene carbon. *Science* **277:** 800-802.

Dissertations in Forestry and Natural Sciences No 133

Maija E. Marushchak

Carbon Dioxide, Methane and Nitrous Oxide Balance of Subarctic Tundra from Plot to Regional Scales

Climate warming and permafrost thaw may lead to increased emissions of greenhouse gases from northern tundra soils. In this work, fluxes of carbon dioxide, methane and nitrous oxide were studied in a subarctic tundra ecosystem. Fluxes were verified at the landscape level by comparing the results of two independent methods and then scaled up over a larger region. The results demonstrate the large heterogeneity of subarctic tundra environment with respect to the green house gas fluxes. Also, a strong, previously unknown source of nitrous oxide is revealed.

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